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THE BEECH FORESTS OF WISCONSIN—CHANGES IN FOREST COMPOSITION AND THE NATURE OF THE BEECH BORDER[1]

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INTRODUCTION

The forests of Wisconsin in which beech (*Fagus grandifolia* Ehrh.) is a component are of particular interest because of the limitation of this species to the eastern part of the state. Although touched upon in several earlier studies, these forests have not been examined throughout their range in the state. A phytosociological study was undertaken to gain information on three primary considerations: the status of the beech forest composition since the early 1800s; the nature of the beech border; and the relationship of present-day forests to other forests of the state without beech. The last of these three is to be reported on in a later paper, with the first two being taken up in the present paper. For these aspects of the study, the records of the original land survey were of primary value in providing information on the presettlement conditions of the forest. Present-day forest composition was compared with that of the past and species behavior along transects across the beech border was studied.

LITERATURE REVIEW

The first ecologically significant mention of beech (*Fagus grandifolia*) in Wisconsin was made by Lapham (1854), who noted the confinement of this species to the vicinity of Lake Michigan in the southern part of its Wisconsin range. He was noncommittal as to any cause and effect relationship. Chamberlain (1877) thought the location of the "Maple-Beech" (*Acer saccharum-Fagus grandifolia*) community was controlled by the isotherms for the summer months and "other elements of the lake influence." Roth (1898) reported beech in the area of Green Bay to be restricted to sandy-loam lands with only scattered invasion of the "real loam or clay lands." Brunken (1900) believed the finest development of beech was to be found on the Kettle Moraine in Washington and Sheboygan counties. These early impressions, although containing some fact, suffer from the limited area of familiarity of the authors.

The surveyors' records as a source of information on early vegetation have been in use about forty years. Shimek (1915) was apparently the first to utilize these data for ecological purposes, and several people have since made similar use of the records. Sears (1925, 1926) used them to advantage in studies in Ohio. Lutz (1930) reported on the original (in the sense of pre-white settlement) forest composition in northwestern Pennsylvania, and Kenoyer (1930, 1940, 1943) mapped the original vegetation of several counties of Michigan. In addition to Sears' studies, survey data from Ohio were applied by Transeau in his study of the prairie peninsula (1935), and Shanks (1939, 1953) used this source of information for studies in that area. Potzger and his associates studied the prairie-forest border in Indiana by this means (Rohr and Potzger 1951, Finley and Potzger 1952, Potzger and Keller 1952), and Elliot (1953) employed the method in a study of second-growth hardwoods in Michigan.

Several studies have been made in Wisconsin, but none have been specific within the area of beech (*Fagus grandifolia*) forests. Finley (1951) mapped the vegetation of the entire state, dividing it into 33 types. Local studies in southern Wisconsin include an analysis by Cottam (1949) of the early vegetation of an area presently in oak (*Quercus* spp.) woods, and a study of the vegetation of Dane County by Ellarson (1949). In northern Wisconsin, Fassett (1944) used survey data in a study of the Brule River basin, and

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Stearns (1949) reported on 90 years' change in a northern hardwood stand.

The literature contains several studies on species at the edge of their ranges. Most striking, and probably most studied, are the transitions from one formation to another, particularly those at timberline and at the prairie-forest border. Studies on the behavior of, and the factors limiting, individual species within a particular formation are much fewer in number. Griggs (1914), studying the behavior of several species in the Sugar Grove region of Ohio, found that many species had abrupt terminations of their ranges, while some showed a gradual decrease. Failing to find consistent correlation of species ranges with any one factor, he concluded that plants of favorable habitats may be limited by the climatic factor, while those of unfavorable habitats are largely controlled by competition. He also emphasized the continuing process of adjustment as reason in some cases for lack of correlation. Hutchinson (1918) attempted to relate limiting factors to the tolerance ranges of the dominant trees of Ontario. For the westward limit of beech (*Fagus grandifolia*) he suggested that the water factor may be limiting, while for its northern limit he believed it to be a matter of time and soil development. Potzger and Keller (1952), in a study of the beech border in Indiana, concluded that the limit of beech is closely related to conditions of soil moisture. Camp (1953, personal communication) expressed the view that this species may be limited in its western extent by a minimum annual precipitation of 30 inches, while to the north it seems to be restricted by growing seasons of less than 100 days.

METHODS

For both phases of the present study, data were copied in a similar manner from the surveyors' record books filed in the Land Office at the Wisconsin State Capitol Building in Madison. Data were transferred from the record books directly to a mimeographed form showing a township gridded into sections. Information on those trees at quarter and section corners was recorded, including the tree species, the diameters, and the distances from the corner. In some of the northern counties, four witness trees were used at the section corners, in which case only the first two trees listed were taken.

The information on the upland trees was used to calculate importance values for the individual species. The basal diameters were converted to basal area and summed for individual species and for all species; per cent relative dominance was then calculated. Each corner was treated as a point and the number of points of occurrence for the various species was used to compute per cent relative frequency. The total number of individuals of all species was used to compute relative density. An importance value for each species was contained by adding the three relative values.

It has been found that a large number of link distances, such as the number recorded in a township, can be averaged to give a reasonably close value for the average distance between the survey trees in feet. The basis for such a relationship was established by the determination that the average of the distances from the point to the nearest tree in each of the quadrants of two closest trees (Q_1 and Q_2) is approximately 66 per cent of the square root of the mean area (Cottam, Curtis, and Hale 1953); the square root of the mean area closely approximates the average distance between trees. The link/foot relationship of 66 per cent therefore allows a direct conversion to the average distance between trees in feet.

Some difficulty in identification was encountered where common names employed by the surveyor

TABLE I. Tree names used by the surveyors and the interpretation given them for this study

Surveyors' name	Probable Species
Balsam, Fir, and Fur	*Abies balsamea* (L.) Mill.
White Maple	*Acer saccharinum* L.
Sugar	*A. saccharum* Marsh.
Maple	*A. saccharum* or *A. rubrum* L. if "Sugar" used by same surveyor
Birch	*Betula* spp.
Y. Birch	*B. lutea* Michx. F.
W. Birch	*B. papyrifera* Marsh.
Bitternut	*Carya cordiformis* (Wang.) K. Koch
Hickory	*Carya* sp. or *C. ovata* (Mill.) K. Koch "Bitternut" used by the same surveyor
Thorn	*Crataegus* spp.
Beech	*Fagus grandifolia* Ehrb.
Ash	*Fraxinus* spp.
W. Ash	*F. americana* L.
B. Ash	*F. nigra* Marsh
Butternut, White Walnut	*Juglans cinerea* L.
Tamarack	*Larix laricina* (DuRoi) K. Koch
Ironwood	*Ostrya virginiana* (Mill.) K. Koch
Spruce	*Picea* spp.
Pitch Pine, Black Pine, and Bastard Pine	*Pinus banksiana* Lamb.
Yellow Pine	*P. resinosa* Ait.
W. Pine, Pine	*P. strcbus* L.
Aspen	*Populus* spp.
'Bap'	*P. grandidentata* Michx.
Poplar	*P. tremuloides* Michx.
Cherry	*Prunus* spp.
W. Oak	*Quercus alba* L.
Swamp Oak	*Q. bicolor* Willd.
Bur Oak	*Q. macrocarpa* Michx.
Red Oak	*Q. rubra* L.
Black Oak	*Q. rubra-Q. velutina* Lam.
Cedar	*Thuja occidentalis* L.
Lynn	*Tilia americana* L.
Hemlock	*Tsuga canadensis* (L.) Carr.
Elm	*Ulmus* spp.

were not precise. "Maple," which could mean either red (*Acer rubrum*) or sugar maple (*A. saccharum*), was sometimes listed. Often this could be interpreted by the use of either red or sugar maple elsewhere by the same surveyor. "Birch" alone necessitated the lumping of white (*Betula papyrifera*) and yellow birch (*B. lutea*). Species of *Ulmus* were listed only as "Elm." Different surveyors, and even individual surveyors, used different names for the same species. For the most part, however, there was a minimum of ambiguity. The names used by the surveyors and the interpretation given them for this study are listed in Table I.

PAST AND PRESENT

For comparison with the early vegetation, data from 14 of the present-day stands sampled by the "random pairs" method (Cottam and Curtis 1949) were assembled. The location of these stands in relation to the beech range is shown in Figure 1. Data from the surveyors' records were selected and copied so as to approximately center each present-day stand in an area equal to one township. Species of trees, diameters, and link distances were recorded from quarter and section corners, with areas designated "swamp" excluded.

To test the homogeneity of the township areas, each was divided into 4 quarters, and a chi-square test applied based on the number of occurrences in each quarter of the most abundant tree of the township. The forest in the township area around Stand Number 7 was eliminated for lack of homogeneity.

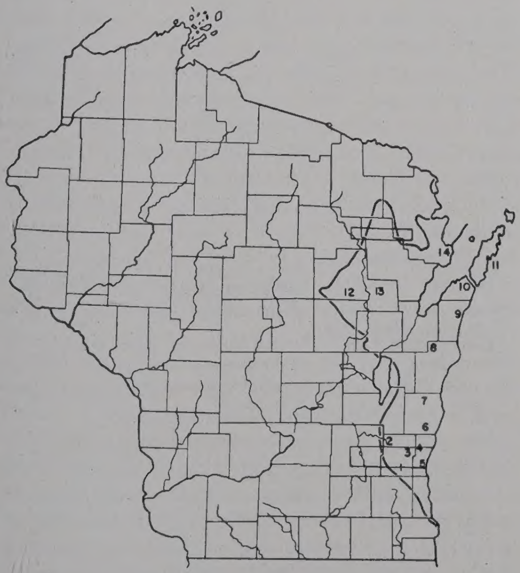

FIG. 1. Location and number of present-day stands used in the comparison with composition at the time of the survey, and the location of transects for analysis of the beech border.

Realizing the probable variability of upland tree composition, it was thought necessary to be rather certain that the trees of a corner to be used were in an area of possible beech (*Fagus grandifolia*). Although the criteria for the present-day stands did not specify minimum amounts of beech, they did require that this species at least be present; some of the upland areas at the time of the survey were quite likely devoid of beech. It would be possible to assure that data used were in an area of beech merely by using only those points that had beech as one or both of the trees. Such an extremely biased sample could hardly be used for comparison with present-day stands, however. It was decided to use data from those points that had species which were present today in a given stand, plus data from points that had species not found today but which were accompanied at the point by either sugar maple or beech; this gave fair assurance that the points used were in an area of possible beech. Using these data, an importance value was computed for each tree species, and the average distances between survey trees were calculated by averaging the link distances.

Results

Table II shows a comparison of the calculated survey importance values with similar data from today's stands. In Table III, the data have been tabulated to show trends for the most important species. The 'Number of Stands' for a species includes only those in which the species had an importance value in either the survey data or the present-day stand; in most instances the species had values in both. In deciding whether a species had shown a significant change in importance value, an arbitrary minimum difference of 16 was chosen. Species which showed a change of 15 or less were classed as 'No Change.' The 'Average Change' was computed from the values for all stands regardless of the amount of difference in importance values.

These changes show no definite correlation of beech behavior with northern or southern position, nor with distance from the beech border. The two stands in which beech increased, Numbers 3 and 4, are in the southern portion of the range, but Stand Number 5, very close to 4 gave a marked decrease in beech. Of the 3 stands closest to the beech border, Stand Number 12 showed a decided decrease, while Stand Number 2 suggests an increase; in Stand Number 1 beech was merely present today and was not reported in the survey data.

TABLE II. A comparison of the importance values computed from the surveyors' records with those of present-day stands

	1		2		3		4		5		6		8		9		10		11		12		13		14	
	1836	1953	1836	1953	1836	1953	1836	1953	1836	1953	1835	1952	1834	1952	1835	1952	1835	1953	1835	1952	1853	1953	1845	1953	1840	1953
Abies balsamea	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	—	—	—	—	—	—
Acer rubrum	—	—	—	—	—	—	4	—	—	—	—	—	3	—	—	—	—	—	—	5	—	—	—	12	—	—
Acer saccharum	111	167	76	235	92	19	96	141	52	127	62	107	61	110	22	93	135	90	84	116	119	210	62	114	24	171
Betula lutea	—	—	—	—	—	P	—	—	—	—	3	—	—	8	5	—	—	—	34	8	—	—	26	15	65	9
					2)								11)								21)					
Betula papyrifera	—	—	—	—	—	11	—	—	—	—	1	—	—	7	5	—	—	66	—	35	—	—	2	—	9	—
Carya cordiformis	—	—	—	—	—	P	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
					2)																					
Carya ovata	—	—	—	—	—	—	10	6	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Fagus grandifolia	—	P	5	17	80	123	64	90	200	123	174	123	136	95	193	200	86	58	80	50	77	47	109	100	152	102
Fraxinus americana	—	—	—	—	5	24	6	26	11	16	8	18	3	6	—	4	—	13	—	4	—	—	4	5	—	18
																					4)					
Fraxinus nigra	2	—	—	—	8	3	3	—	2	—	—	—	8	3	5	—	—	—	—	—	—	—	7	—	—	—
Ostrya virginiana	19	13	35	7	8	41	26	6	7	4	11	3	12	6	—	4	—	9	8	23	15	22	8	9	—	—
Pinus strobus	—	—	—	—	—	—	—	—	—	—	—	—	6	—	—	—	—	—	6	10	—	—	31	11	10	—
Populus spp.	—	—	—	—	2	P	—	—	—	—	—	—	10	P	—	—	—	—	—	—	—	—	8	—	3	—
Prunus spp.	2	4	—	—	—	—	—	5	—	8	—	8	—	—	—	—	—	—	—	—	—	—	2	—	—	—
Quercus alba	74	57	57	11	10	—	—	—	4	P	13	—	—	—	—	—	—	—	—	—	—	—	—	—	3	—
Quercus rubra-velutina	48	53	16	—	14	P	25	P	—	—	4	23	3	P	—	—	—	11	—	7	—	—	5	4	—	—
Tilia americana	7	—	73	15	48	39	34	12	22	22	13	14	5	—	11	P	35	23	31	13	37	13	—	25	4	—
Tsuga canadensis	—	—	—	—	—	—	—	—	—	—	—	—	33	67	59	—	45	30	56	27	11	—	32	6	31	—
Ulmus spp.	36	4	38	16	28	38	34	13	2	P	11	4	8	—	—	—	—	—	—	—	16	8	5	—	—	—

TABLE III. Trends since the time of the survey for the most important species

	CHANGES IN IMPORTANCE VALUES				
	Number of stands	Number of stands showing			Average change
		Increase	Decrease	No change	
Acer saccharum	13	11	2	0	54 increase
Fagus grandifolia	12	2	7	3	19 decrease
Ostrya virginiana	12	1	2	9	0
Quercus alba	6	0	2	4	16 decrease
Q. rubra-velutina	9	1	2	6	2 decrease
Tilia americana	13	1	4	8	11 decrease
Tsuga canadensis	7	1	4	2	20 decrease
Ulmus spp.	9	0	3	6	11 decrease

Discussion

What is the reality of these changes? Has beech (*Fagus grandifolia*) actually decreased in density or has it perhaps maintained itself, while sugar maple (*Acer saccharum*) has increased in density to the extent that beech, on a relative basis, seems to have decreased? Taking into consideration the various factors influencing the surveyors' choice of trees and the resultant effect on the distance between survey trees, a comparison of the average distances between those trees and the trees of today indicates little or no change has taken place in this respect. The change, therefore, is not one of density but of composition, with beech showing a general decrease and sugar maple a marked increase. Evidence from a single stand is only suggestive; from several stands it is fairly convincing.

Such a trend is not unique to Wisconsin. Wollett and Sigler (1928), in a comparison of undisturbed "beech-maple" (*Fagus grandifolia-Acer saccharum*) forests of northern lower Michigan with reforested areas, found that sugar maple was notably more dense in the reforested areas while beech was definitely less abundant. Elliott (1953) in an analysis of the surveyors' records in the same general area found that woods which were beech-hemlock-sugar maple (*Fagus grandifolia-Tsuga canadensis-Acer saccharum*) at the time of the survey were now predominantly sugar maple, with beech reduced to secondary importance. Kenoyer (1930) studied land survey data from southeastern Michigan and concluded that beech was more numerous in the early 1800s than at the time of his study. Cain (1935) also concluded that beech was decreasing in southern Michigan.

Shanks (1953), working in the beech-maple region of western Ohio, reported considerable change in the forest remnants of the area from that reported in the survey a century prior; beech showed little evidence of the high importance level it had at the time of the survey.

We should examine possible explanations for the decline of beech. Cain (1935) suggests that a lowering of the water table accompanying removal of much of the timber vegetation may be important with respect to the decrease of beech in Michigan. Elliott (1935) attributes the decrease of beech in Michigan partly to selective cutting. Records from Wisconsin, however, indicate that beech wood has been consistently low in economic value with other species much preferred.

Ostenfeld (1932) in a report on the beech (*Fagus sylvatica*) forests of Denmark speaks of soil impoverishment by nearly pure stands of beech to the extent that it cannot regenerate itself. A comparison of the nutrient element content of freshly fallen litter of the American beech shows it to be inferior to sugar maple and other deciduous species with respect to calcium content (Lutz and Chandler 1946). The enrichment by sugar maple would do much to counteract any trend of soil depletion, however.

As with most species of the edge of their range, beech is probably seldom in a static condition, but rather in a continuing state of attempted adjustment with the fluctuations of the climate. A prolonged period of increasing warmth might be expected to bring about a decline in beech, particularly if not accompanied by an increase in moisture. Sugar maple, on the other hand, with its wider tolerance to decreased precipitation-evaporation ratios, would likely show an increase in importance.

What evidence is there for such a climatic change? Certain Europeans have evidence that their continent is in the midst of a period of increasing warmth (Angström 1939, Labrijn 1950), and several people, including these men, believe that a similar warming is occurring in temperate North America. Brooks (1926), using tree ring widths of California sequoias (*Sequoia gigantea* (Lindl.) Decue.) as part of his evidence, concluded that major climatic shifts in the temperate regions of Europe and Asia are concurrent with shifts in temperate regions of this continent. He acknowledges that these trees are near the southern edge of the temperate zone.

Evidence from North America itself is thought by some to indicate a general trend of increasing winter temperatures (Kimble 1950, Hare 1951, Brooks 1953). Much of the evidence of these climatologists is derived from a comparison of conditions of the last half of the 19th century with the climate since 1900. Kincer (1933), doubting the reality of an upswing in temperatures, contended that the cold period of the 1800s was only a dip and that temperatures preceding this were much as those of the period after 1900.

The weather records in the area of this study are short-term and inconclusive, but there seems to be little evidence to support any definite upward trend. When viewed through the numerous pronounced fluctations, the curves for winter temperatures since 1900 are essentially level.

The possibility that the cold period of the 1800s may itself have been important in reducing the beech population can be largely dismissed for lack of indication of "recovery" in the fifty-odd years of warmer temperatures since then.

There is some evidence which suggests that the mast production by beech was higher in the past than in more recent times. Any marked change in this respect would eventually be felt in the tree population. Schorger (1949), in an analysis of available food for squirrels in early Wisconsin, found reports of heavy beech nut crops during several years in the 1800s; 1853, 1865, 1875, 1877, 1879, 1887, 1889, 1891, 1893 are listed as having heavy mast production in one or more counties. Similar evidence is available from the Adirondacks where Merriam (1884) reported good beech nut crops in the alternate years beginning with 1871 and ending with 1883.

It is possible that the reported heavy mast production was characteristic of relatively open-grown trees, as is the case with the European Beech (*Fagus sylvatica*) (Watt and Tansley 1932), and was not much more abundant then than now on trees in closed canopies. It seems likely that open-grown trees were relatively rare, however, in view of the susceptibility of the American beech to sunscald (Potzger 1941, Spaulding and Bratton 1946, Eyre and Zillgitt 1953).

The alternate year pattern should be considered. It may be similar to a phenomenon seen in fruit trees, where following a few fruitless years a large amount of material is stored up and a heavy crop is produced the first subsequent year of fruiting. The depletion by this crop is such that only a small crop is produced the following year, but by the second year reserves and consequent fruiting are again high. Although continuing through several years, this pattern does not necessarily mean greater production when considered on a per year basis.

A suggestion that merits investigation concerns the effective distance that beech pollen can travel and the possibility of self-sterility. If, through abundant root sprouting, the populations of relatively small areas, such as present-day stands, have become genetically similar, and if self-sterility is the case, it might be that the extensive timber cutting has resulted in isolated populations with a much reduced potential for production of viable seeds because of the lack of pollen from genetically different trees. Evidence for this or something related was found in the abundance of empty nuts. In many instances, it was quite easy to gather a hundred nuts in a fairly small area, but examination of the inside showed that the large majority were completely empty and only an occasional one was filled out with a well-developed seed. There was seldom any indication of insect damage.

Another possibility should be mentioned even though there is little evidence for or against it. We have thus far been concerned primarily with beech, but has there perhaps been a genetic change in sugar maple which has enabled it to gradually replace beech? Introgression with black maple (*Acer nigrum* Michx. f.), for instance, might result in some sort of hybrid vigor which could bring this about.

The explanation for the consistent decrease of other species, in addition to beech, in all likelihood, lies in large part with succession. Beech, however, is generally considered to be as climax as sugar maple; Eyre and Zillgitt (1953) feel that it may be even more so. But is it? Certainly from a reproduction standpoint, beech does not approach sugar maple. Nowhere in Wisconsin are beech seedlings numerous, whereas sugar maple reproduces abundantly in this way. A survey of the seedling population in several stands strongly suggests that beach germination and seedling survival are best in areas where a fairly heavy, mor type of humus is to be found; usually hemlock (*Tsuga canadensis*) is rather high in importance and is itself reproducing to some extent. On areas of mull humus, beech seedlings are much less frequent. Conversely, sugar maple shows only minor success on mor humus, but demonstrates a very prolific nature on areas of mull humus.

The relationship between high seedling production and high population of a particular species is immediately evident. Between two otherwise reasonably similar species, the one most apt to fill an opening will be the one with the greatest number of contenders. Beech quite possibly was at a relatively high level of density at the time of the survey because of previously abundant seedling germination and survival. With a gradual decrease in seedlings, a similar decrease in trees would follow, particularly if sugar maple at the same time was increasing its seedling production.

Available evidence does not allow positive statements about the vegetational change previous to the indicated shift from beech to sugar maple, but it is worthwhile to consider one possibility. Although the exact successional relationships between beech and hemlock have not been worked out, there is some evidence that beech is more climax than hemlock in this area (Brown and Curtis 1952). Conceivably, prior to the high importance level of beech, there was an abundance of hemlock, with conditions quite suitable for beech germination and increase. Beech gradually replaced hemlock, and the predominant type of leaf falling to the forest floor shifted correspondingly. The microbial population, the rate of decomposition and ultimately the type of humus changed, perhaps from a mor to a mull type. This possibility is suggested by the occurrence of humus intermediate to these two types in several of the northern beech-maple stands. The need for research on this matter, particularly in these stands, is apparent.

As the mull type was more nearly approached, the failure of beech and especially hemlock became greater and the success of sugar maple more common. The transfer in understory dominance was in time carried up to the tree population, with part of this change being apparent in the present comparison with data from the surveyors' records.

This hypothesis of succession from hemlock to beech to sugar maple, admittedly very tentative, is perhaps more reasonable for the beech forests of the northern part of the state where hemlock is abundant, but it should be borne in mind that the northern conifer element reaches its most southerly extent in the eastern part of the state where beech is found.

An analysis of the reproduction here and in other areas gives some indication as to the future of beech. Clayberg (1920) in a quantitative study of a sugar maple-beech woods in northern lower Michigan found that small saplings of sugar maple exceeded those of beech almost 10 to 1. Cain (1935) found a similar preponderance of sugar maple saplings in a southern Michigan woods, in which beech was the most important species in the tree class. Similar findings have been reported from Indiana by Esten (1932), Potzger and Friesner (1943), Keller (1945), Jones (1952), and Trotter (1952).

In Wisconsin, some stands had greater relative densities of beech saplings than of sugar maple, and in a few cases this occurred where sugar maple was most important in the tree stratum. However, the characteristic habit of root-sprouting probably accounts for the great majority of the beech saplings here and in the other areas mentioned. The occurrence and importance of suckering in beech has been noted by Illick and Frantz (1928), Williams (1936), Egler (1940), Hough and Forbes (1943), and Camp (1953, personal communication), and the habit was observed to be extremely common in the stands of this study.

It seems logical to conclude that although less abundant now than in the past, beech will maintain itself as part of the sugar maple-beech forests, partly by occasional seedling survival and maturation, but mainly by vegetative reproduction. It is the general level at which beech will maintain itself which is in doubt.

THE BEECH BORDER

The information from the land survey was further used in the study of the beech border. In order to picture the transition across the border, east-west transects were laid out in the north and the south to include areas in and out of the beech range. The area of the transects in relation to the approximate western limit of beech is shown in Figure 1. The area of the southern transects was surveyed in the years 1834-1837, and that of the northern transect from 1853-1857.

Southern transects

In the south, two adjacent transects were used, each 1 township in width, running from Lake Michigan westward a distance of 9 townships. Each township was treated as a unit within which importance values were computed for each upland tree speces. Because the curves for individual species behavior in the two transects were so similar, the values in both were averaged and a single plot was made. The curves for 4 of the most important species are shown in Figure 2.

Beech shows a rather even and rapid decline west from Lake Michigan, not being recorded west of Range 17 E. Sugar maple and basswood (*Tilia americana*) show a general increase to the Rock River, where both species decrease sharply in importance; both species were recorded west of the river, but in an area protected by small streams. Bur oak (*Quercus macrocarpa*), on the other hand, was recorded only once east of the Rock River, and shows high importance immedi-

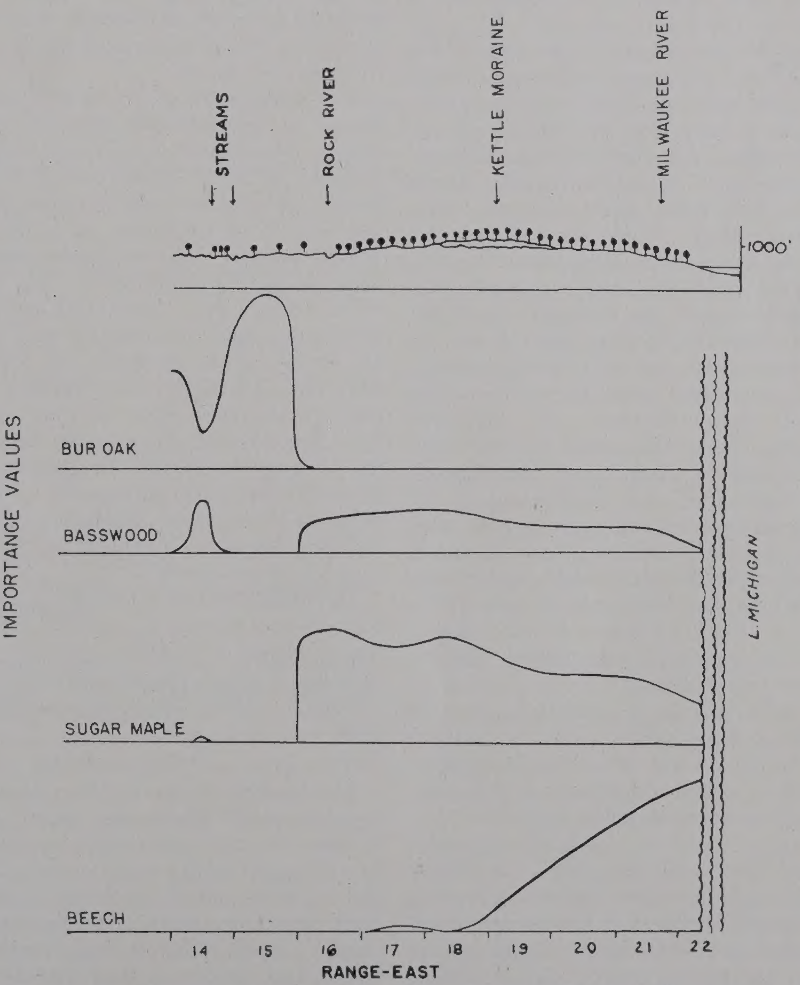

FIG. 2. The average importance values for the four most important species in the two southern transects.

ately west of the river. It should be noticed that the importance of this species drops noticeably in the area bounded by streams.

The abruptness of the change at the Rock River is further seen in the average distances between survey trees (Table IV). No significant variation appears from Range 22 E. to the middle of Range 16 E., but immediately west of the river, the distances between trees show a very great increase.

Table IV. The average distances between survey trees in the two southern transects

	Range - East										
	14		15	16		17	18	19	20	21	22
10N. . .	103	44	99	132	35	24	32	30	30	30	31
11N. . .	88	44	114		38	27	32	33	33	33	30
	Streams			Rock R.							

Discussion.—In each transect, the curves for bur oak, basswood, and sugar maple suggest disturbance of some kind. It is well-established that Indian populations were high at various times in southern Wisconsin, and there is ample evidence that they used fire for various purposes, such as clearing brush and driving game. This is a type of disturbance which could account for the sharp changes shown by these species. The behavior curves suggest that fires were quite destructive from the west, the direction of prevailing winds, to the Rock River, resulting in the virtual elimination of basswood and sugar maple, and allowing the much more fire-resistant bur oak to attain high importance. To the west of the river, the occurrence of basswood and sugar maple only in stream-bounded areas adds support to the fire hypothesis. An examination of the river and stream widths is suggestive of their relative value as barriers. The westernmost stream was recorded as 80-100 feet in width by the surveyors, and its smaller neighbor to the east, 10-15 feet. The Rock River, on the other hand, varied around 225 feet in width, a formidable distance for fire brands to traverse.

The case for fire as an explanation for the abrupt behavior of these species seems very strong, and in view of the absence of any decided physiographic, edaphic, or climatic changes at this point on the transect, it seems almost indisputable.

The behavior of beech is less easily explained. If areas west of its termination were climatically suited for its growth, it might be expected to show a behavior similar to that of basswood and sugar maple, although beech because of its thin bark is perhaps more susceptible to fire. The possibility exists that fires of lesser intensity and extent occurred to the east of the Rock River, and the beech, being more sensitive, was thereby limited.

Evidence against fire as the limiting factor for beech is rather convincing, however. If beech had been burned out of the areas between the Rock River and the Kettle Moraine, while being protected to the east, it would be expected to reestablish itself with the cessation of fire, particularly since conditions remained, or at least had again become, suitable for abundant sugar maple. There is little evidence of past or present aggressiveness on the part of beech; it has not moved back and there is no indication that it is doing so today.

Other somewhat related possibilities with respect to fire should be mentioned. Beech may have been removed by this factor but was not able to return because of previous or subsequent climatic change, or perhaps because of settlement by white man. If such is the case, the particular factor is in reality the limiting factor. Fire merely hastened the retreat.

The topography of the Kettle Moraine itself should be considered, as the decline in beech is more or less coincident with its location. The occurrence of beech stands on other areas of the Kettle Moraine indicates their absence here cannot be due to roughness of terrain. Brunken (1900) thought their best development was to be found on the Kettle Moraine.

The soils in the transect area are quite similar, with no apparent correlation with the decrease and dropping out of beech. A few miles west from Lake Michigan, there occurs a strip of reddish or grayish-brown clay and loam of the Kewaunee-Poygan series, while the remainder of the transect is yellowish or grayish-brown loam of the Miami-Bellefontaine series. The occurrence of several beech stands today on areas of Miami-Bellefontaine soils discounts the idea that these soils would limit beech.

The individual factors of fire, physiography, and soil do not provide a suitable explanation for the restriction of beech, nor does a combination of these. Climate, the next logical factor for consideration, will be discussed in the following section.

Northern transect

The location of the northern transect was selected so as to picture the nature of the beech boundary to the east as well as to the west (Fig. 1). It begins on the east in an area of pine woods and no beech, moves west into an area of moderate beech importance, and terminates out of the range of beech. These changes occur in the relatively short distance of about 18 miles. To establish the trend on either side of beech, the transect was made 5 townships, or 30 miles, in length.

For greater sensitivity along the transect, the townships were divided in half with respect to north-south axes. Each half was treated as a unit and importance values were computed for the various species; the values were then plotted along the transect (Fig. 3).

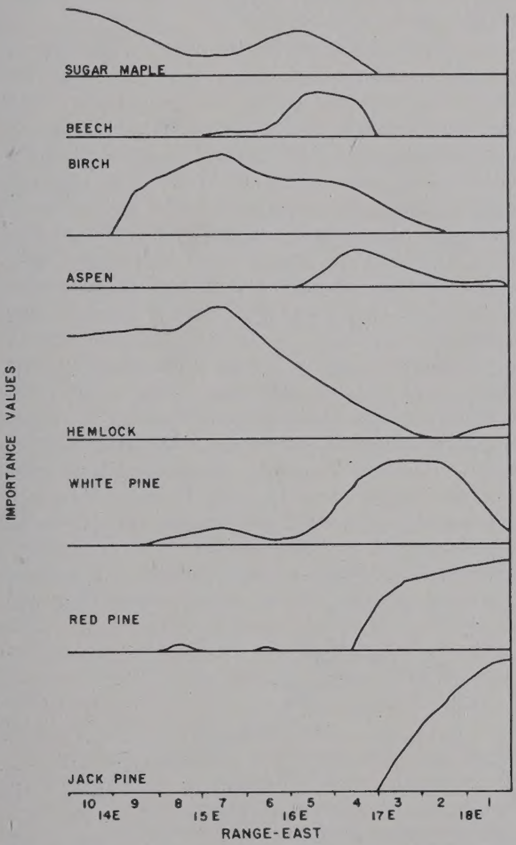

Fig. 3. Importance values for the most important trees in the northern transect.

Of most importance in the unit to the extreme east are jack pine (*Pinus banksiana*) and red pine (*Pinus resinosa*). White pine (*Pinus strobus*) is of lesser importance, but these three species together make up a total importance value of 280.3 out of the possible 300.0; hemlock (*Tsuga canadensis*) shows slight importance, but beech and sugar maple are notably absent.

Moving west, jack pine drops off rapidly, while red pine shows a slight immediate drop, and white pine rises substantially. The three species predominate for a distance of a township and a half. Beyond this red pine is of very minor importance, and jack pine was not reported. White pine remains fairly high.

Complimentary to the sharp change in jack pine and red pine are the patterns for hemlock, sugar maple, and beech. The intergradation of these species with the above two pines is very slight. White pine, however, is still quite important in the area where the deciduous species and hemlock appear, but decreases in importance rather soon to the west. Hemlock shows a consistent rise to a high importance value and levels out. The trend for sugar maple is rather irregular, but shows a general rise, and is increasing at the western end of the transect.

Beech shows an abrupt level of importance against the dropping out of jack pine and red pine, and shows an almost equally sharp change as it drops out to the west, tailing off only slightly in this direction. It should be pointed out that an equally sharp transition occurs between pine and beech as one moves east from the pine maximum.

"Aspen," which could be *Populus grandidentata* but more likely is *P. tremuloides*, shows a rather even rise and fall across the pine-beech transition. Birch (*Betula*) is increasingly important westward, reaching a high point with hemlock, but dropping out completely before the end of the transect. Yellow birch (*Betula lutea*) was listed in the western two townships and white birch (*B. papyrifera*) in the easternmost township; those in the middle were listed only as "birch." The pattern for white birch may be similar to that of aspen, with a gradation into yellow birch to the west.

Discussion.—There are several things about the curves which need to be explained: the sharp transition from the shade-intolerant pines to the tolerant deciduous trees; the rather sudden drop in beech to the west and the accompanying dip in sugar maple; and the lack of beech further to the west where sugar maple is again high in importance.

Table V, showing the average distance between the survey trees and the average basal areas, adds to the picture of the forest transition. The trees in the area of pine are large on the average, but as shown by the values for distance between survey trees are exceedingly scattered. In sharp contrast to this are the values for tree distances west of the area of pine. No longer a savannah condition, the spacing of trees is probably similar to that found in present-day closed canopy stands. The change in tree spacing coincides with the equally abrupt transition from pine to the shade-tolerant deciduous species.

Table V. The average distances between survey trees and the average basal areas in the northern transect

	Range - East									
	14		15		16		17		18	
Aver. dist. between survey trees	25	27	22	16	22	21	24	33	83	99
Aver. basal area........	187	182	137	101	126	93	147	191	169	149

As in the southern transects, a suitable explanation must account for this marked change in composition. The topography shows no correlative difference along the transect. The soils in the area of pine are Vilas sands, while those in the western portion of the transect are considerably heavier soils of the Kennan series. This soil difference may enter into the explanation of the change in composition, but it alone does not provide the answer, as beech and sugar maple are abundant to the east of the pine maximum on similar Vilas sands. There is no evidence of climatic change along the transect which could account for this particularly sharp transition.

Fire is recognized by several workers as one of the primary factors responsible for high importance levels of pine (Maissurow 1941, Brown and Curtis 1952, Spurr 1954). Substantial evidence for fire as the principal cause for the present situation is found in the surveyor's records, where recorded are such observations as: "Timber scattering, Pine having been mostly destroyed by fire." (Foster 1856.) Associated with fire may have been the previously mentioned soil difference; burned areas of light, sandy soils tend to remain in pine for a longer time than areas similarly burned but with a heavier soil.

West of this sharp transition, fire again may have been a factor, but if so probably only in a minor way. The dip in sugar maple corresponds to peaks for hemlock and birch and to secondary occurrences of white and red pine; fire may well have been the cause of this. It is possible that in this area, beech was also reduced in importance by fire. We are mainly concerned, however, with the absence of beech further to the west where conditions were again favorable to sugar maple but evidently not for beech. Neither soils nor topography provide an explanation for the absence of beech, the attention again being turned to climate.

Correlation of weather station climatic data with gross vegetational boundaries is difficult; with a single species, it is usually impossible. What is apparently limiting in one part of the range may be quite different from the controlling complex in another part of the range. Analysis of climatic conditions within the Wisconsin beech range is also complicated by the fact that 8 of the major weather stations within this range are near fairly large bodies of water. Obviously, the exact relationships of the beech in Wisconsin to climate must wait for through macro- and microclimatic studies within the forests themselves.

In spite of these limitations, some indication of climatic similarity or dissimilarity between the beech and non-beech areas can be obtained from standard weather station data. For purposes of comparison, areas northwest and southwest of the beech range were delimited by arbitrarily drawn contour lines fifty miles beyond the beech border (Fig. 4). The data for all stations within an area were averaged to obtain mean values for individual factors. Data from corresponding southern and northern beech and non-beech areas were then compared (Table VI). In the south, the annual precipitation in and out of the beech range is quite similar, and likewise the annual precipitation. The January and July temperatures, however, indicate a greater range of extremes to the southwest of beech. Warmer summer temperatures to the southwest would tend to result in increased evaporation and thus lower precipitation effectiveness. The isopleths for Thornthwaite's Precipitation-Effectiveness Index (Finley 1951) indicate an east-west gradient more or less paralleling the

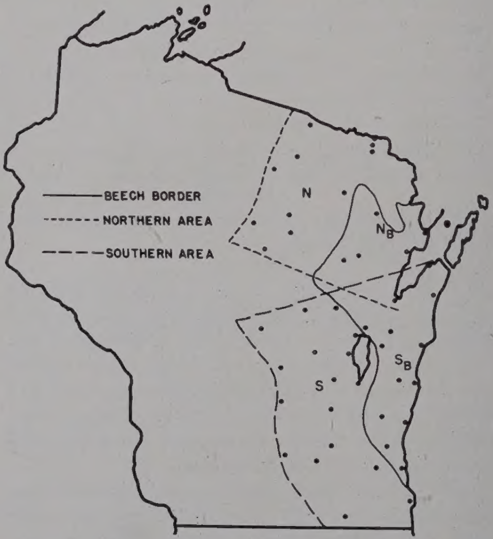

Fig. 4. Areas of beech and non-beech used for comparison of climatic data, and the location of weather stations.

TABLE VI. Mean values for comparative climatic data from beech and non-beech areas

	NORTHERN AREA		SOUTHERN AREA	
	Beech	Non-Beech	Beech	Non-Beech
Aver. ann. precip.	28.72	29.72	29.18	30.77
Aver. ann. temp.	44.0	40.8	45.1	45.9
Aver. July temp.	69.3	67.7	70.3	73.0
Aver. Jan. temp.	16.3	12.6	18.8	17.0
Aver. growing season (days)	141	114	—	—

beech border. The critical point of moisture tolerance for beech may well be related to such a gradient.

In the north, the annual precipitation is again quite similar in and out of the beech range, but the temperature data show notable differences. The beech area appears to be substantially warmer than the area immediately to the northwest. The mean growing season is perhaps particularly significant, averaging over 25 days longer in the area of beech. Growing season data based on temperatures of both 32° F. and 28° F. at ground level (Wang & Suomi 1955) indicate a sharp reduction from Green Bay to the northwest.

SUMMARY

In Wisconsin, the American beech (*Fagus grandifolia*) is of particular interest because of its confinement to the eastern part of the state. Using the records of the original land survey as the primary source of information, the composition of present-day beech forest remnants was compared with that of the past, and the nature of the beech border was analyzed.

Importance value data from present-day stands were compared with similar data computed for the trees in an area of approximately one township about each of 13 stands. The data indicate a substantial increase in the absolute density of trees per acre for sugar maple (*Acer saccharum*) since the early and mid-1800s, while in the same period beech and most other upland species have shown a decrease in density and importance. These changes seem to be general throughout the Wisconsin beech range.

Several possible explanations for the decline in beech are suggested and evaluated. They include: climatic change of a nature unfavorable to beech; a decrease in viable beech mast; hybrid vigor in sugar maple as a result of introgression; and long-term succession in which sugar maple gradually attains predominance. For none of these is the evidence conclusive, but the matter of succession is perhaps most deserving of concentrated study, particularly since some doubt is cast upon the general assumption that beech in this area is as climax as sugar maple. The possibility of a successional shift in dominance from hemlock (*Tsuga canadensis*) to beech and finally to sugar maple is suggested.

Species behavior in transects across the beech border in the southern and northern portions of the beech range were studied. In the southern transect, it was evident that fire had been an important factor in the area, particularly to the west of the beech range. A sharp drop in sugar maple and basswood (*Tilia americana*), and an abrupt rise in bur oak (*Quercus macrocarpa*) importance are accountable to this factor. The decline in beech, however, could not be correlated with fire, nor could it be explained by differences in soils or topography. In the northern transect, the susceptibility of beech and sugar maple to fire was apparent, with both species showing sharp transitions with areas of pine known to have been burned. To the west, beech showed a rather even decline coincident with a general rise in sugar maple importance. In both the north and the south, it appears that climate is the primary factor limiting beech.

Certain climatic factors suggest themselves as being part of the climatic complex limiting beech. The northwestward limit of beech seems to be correlated with a decrease in temperature and the growing season, while a reduction in moisture effectiveness may be limiting for its southwestward extent.

It is concluded that the beech border is relatively stable in position and that, although less abundant now than in the past, beech will remain a part of the climax forests of the area, due in large part to its habit of root-sprouting.

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EVAPORATION FROM FOREST SOILS NEAR DONNER SUMMIT, CALIFORNIA, AND A PROPOSED FIELD METHOD FOR ESTIMATING EVAPORATION

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Introduction

The measurement of evaporation from the earth's surface has devolved to several quite standard methods or techniques depending upon the accuracy of "measurement" (actually, approximation) desired by the worker for his study. The theories behind these several methods vary from complex mathematical statistical theories of turbulence to simple linear correlations of two or three variables (Anderson *et al.* 1950, Water Loss Investigations 1952). As might be expected, the complex approaches require equally complex instrumentation, and results are constantly under fire from opponents of the particular approach. The less complex techniques are not very elegant mathematically, but they have consistently given quite useful and apparently quite valid results with relatively little in the way of instrumentation (Anderson *et al.* 1950: 67). Despite the fact that simple approximation methods, such as the "vapor pressure deficit" approach, frequently give more usable and probably equally accurate results, these methods also come under fire (Thornthwaite 1940). Often the criticisms lack a constructive aspect, and under certain circumstances serve only to becloud the issues. This paper is an attempt to place the standard ecological evaporation techniques in a more encouraging light and to suggest a few modest improvements.

The Vapor Pressure Deficit Approach

The term "Vapor Pressure Deficit" has been used to mean either the difference between the saturation vapor pressure of the air and the ambient vapor pressure of the air $(E_s - E_a)$; or the difference between the saturation vapor pressure of a water or land surface and the ambient vapor pressure of the air $(E_b - E_a)$. The original statement of this variable as a measure of evaporation (rate) seems to have come from Dalton (1802) when he proposed a simple equation for evaporation rate from a water surface:

$$V = C(E_w - E_a) \qquad (1)$$

V = evaporation rate (mass per unit area per unit time)

E_w = saturation vapor pressure of water surface

E_a = ambient vapor pressure of free air near water surface

C = a proportionality factor most frequently formulated as a function of the barometric pressure at the station and the mean wind speed at which E_a is taken.

Since the measurement of a surface temperature can become quite a touchy problem, Penman (1949) points out that it is generally advisable to measure and use the other form of vapor pressure deficit in approximating evaporation rates: the expression $(E_s - E_a)$ referred to above, using the saturation vapor pressure of the air near the surface. An example of the use of this latter version of vapor pressure deficit in approximating evaporation appears in a recent study by Kucera (1954) in which an empirical expression of the form:

$$V = A + B\,(E_s - E_a) + Cu \qquad (2)$$

was derived where:

V = evaporation rate

$(E_s - E_a)$ = vapor pressure deficit as just described,

u = wind speed near the ground, and

A, B, C = constants.

Thornthwaite (*op. cit.*) goes to great pains to show why relationships such as (2) cannot physically be depended upon to give reliable measures of evaporation rate. Specifically, he cites several examples, in which an increase in the vapor pressure deficit, of the form $(E_s - E_a)$, could be accompanied by a decrease in evaporation rate, and vice versa. These hypothetical situations are completely correct as given, but one finds on further consideration that such situations are quite uncommon in nature. That is, V and $(E_s - E_a)$ generally change in direct proportion to one another in natural situations; so that although equation (2) cannot be rigorously derived, it is nevertheless quite dependable and useful in most commonly occurring environments.

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So, we have mentioned two general relationships, (1) and (2), upon which most of the standard field methods for approximating evaporation rate are based. A simplification of (2) which is frequently observed to give good results may be written:

$$V = B\,(E_s - E_a) \qquad (3)$$

where the symbols are as before and the wind is ignored. Now let us examine a study which makes use of these relationships.

Observations of Evaporation from Forest Soils

The evaporation studies described below were originally carried out in an attempt to devise a method of estimating quantitatively the evaporation from soils in a specific area by means of a few simple instruments and records. In this case, the area is near Soda Springs, California, just west of Donner Summit, at an elevation of about 7,000 feet in the Sierra Nevada. (Fig. 1.)

The study was begun by placing an evaporation station in a semi-open site such that almost no direct sunlight would fall on it, but with almost complete freedom of horizontal wind movement near the ground. A pan having a 1000 cm² cross-sectional area and approximately 10 cm in depth was filled with soil and litter in as natural an arrangement as possible, and then the pan and soil were placed snugly in the resulting hole in the forest floor. The effect was to be that of introducing the pan into the plot without disturbance of the litter consistency or subsoil arrangement. That this was accomplished might be evidenced by the fact that two small pine seedlings continued to grow in the pan during the entire experiment at this site.

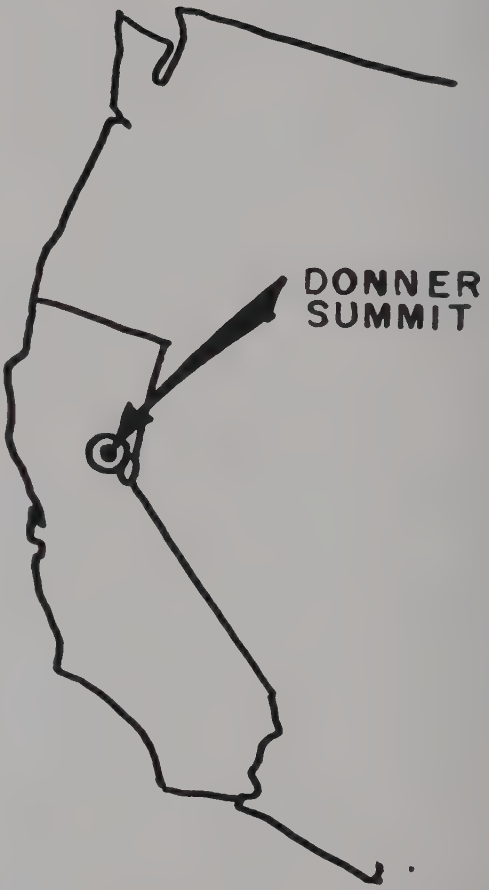


Fig. 1. Location map—Donner Summit, California.

This station was located beneath a clump of trees at the edge of a park-like stand of mixed pine and fir of mature second-growth with an average height about 50 feet. This edge of the stand was near the bank of a mountain stream, and the effect was that of the pan being beside a wind channel in trees having almost no branches lower than the average midwinter snow pack depth of about 8 feet. (Fig. 2.)

At odd intervals, the pan was lifted from its berth and weighed at once on a triple beam balance graduated to the nearest gram. At the same time, a Weston bimetallic thermometer (0-100°F.), the long axis of whose sensitive element had been left about 3 cm below the soil surface in the pan, was read, the temperature recorded, and the pan replaced.

Also, on the ground next to the pan was placed a standard Weather Bureau instrument shelter housing a Friez USWB hygrothermograph with a weekly chart.

After 8 days of record had been taken with this setup, the shelter and instrument were moved to such a position that the hygrothermograph was 4 feet above the pan and still in a zone of almost unrestricted horizontal wind movement. A similar

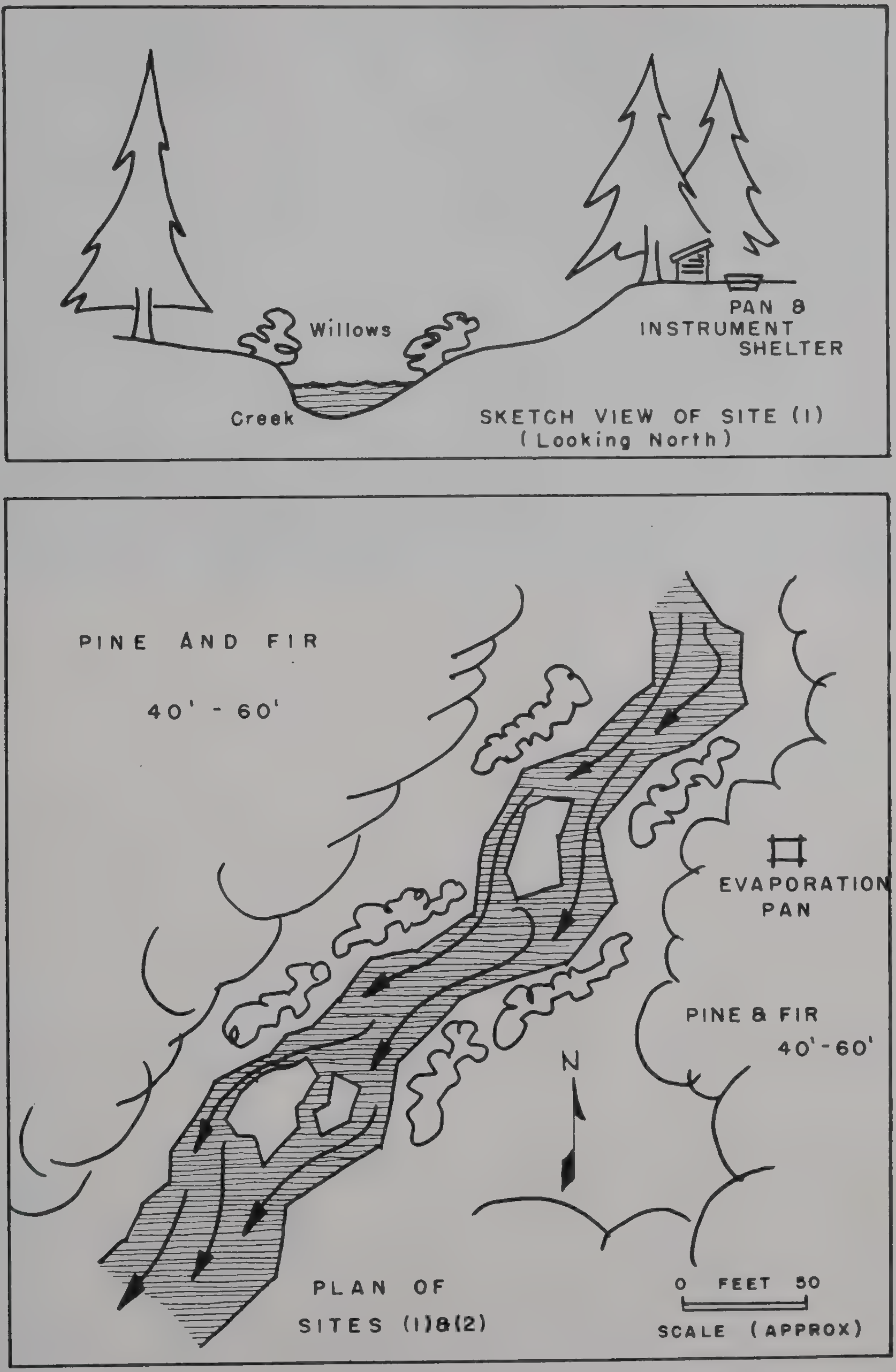

Willows
PAN & INSTRUMENT SHELTER
Creek
SKETCH VIEW OF SITE (1)
(Looking North)
PINE AND FIR
40' - 60'
EVAPORATION PAN
PINE & FIR
40'-60'
N
PLAN OF SITES (1)&(2)
0 FEET 50
SCALE (APPROX)

Fig. 2. Sketch of Site (1).

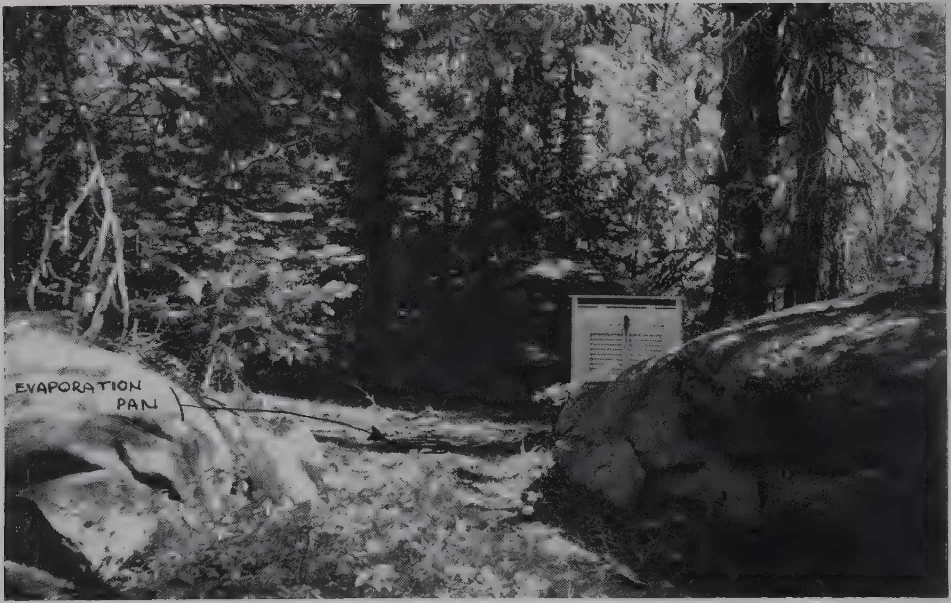


Fig. 3. Site (3) looking east.

length of record was taken with this arrangement, followed by several replication periods with the instrument once more on the ground.

In order to obtain comparable data from an environment having different physical attributes, a new station was established nearby in a small clearing (approximately 20 ft x 10 ft) in a dense stand of pine and fir having almost complete restriction of horizontal wind movement near the ground. (Fig. 3.) Several periods of record were taken here in a manner identical to that at the first site, but no measurements were made in the wooded site with the instrument off the ground surface.

Hereafter, the presentation of data will be grouped and designated as follows (with the dates of the periods of measurement):

Site description	*Site no.*	*Dates*
Semi-open, instrument on ground	(1)	7/1-9/52
		8/8-12/52
		8/15-20/52
		8/26-30/52
Semi-open, instrument at 4-foot level	(2)	7/9-17/52
Clearing in dense stand, instrument on ground	(3)	9/1-9/52
		9/15-22/52

The soil in the pan was not artificially watered, and no major amounts of precipitation fell during the individual periods of measurement. The few rainstorms of the summer occurred between observation periods. Since the period of the experiment was the summer following the largest winter's accumulation of snow on record in the area, the soil in and near the pan remained moist at all times.

A scheme was then devised to use these data in a formula of the form (1) as derived by Fitzgerald (1886):

$$V = (0.40 + 0.199\,u) \cdot (E_w - E_a)$$

V in inches per day
u in miles per hour
E_w, E_a in inches of mercury

In order to obtain values to use in this formula from the data collected, the procedure followed was simple, though relatively crude. First, a value for the wind speed was assumed, constant for all periods of observation. A value of 0.1 mph was taken as a general approximation in accord with extensive data measured in the immediate area by well-instrumented network of the Corps of Engineers, U. S. Army, and reported by Miller

(1952) as being typical of this height (0.5 meters) in this type of forest stand. Next, a time of day plot was made (Fig. 4) of the difference between the soil temperature and the air temperature (instrument at ground level) for each single observation made at Site (1). Through these points a smooth curve was drawn and assumed to be the invariant march of soil temperature relative to air temperature on every day of the record at that site.

For temperature and moisture data to be used in the calculations, mean temperature and relative humidity values were tabulated for each two-hour period according to the hygrothermograph charts. For each two-hour period, then, a mean saturation vapor pressure was determined by the mean temperature, and a mean ambient vapor pressure was determined by the product of mean relative humidity and mean saturation vapor pressure. A mean of the ambient vapor pressure for the observation period, with proper weighting allowance made for fractions of two-hour periods occurring in the observation period, was then taken as E_a for the period.

With no continuous record of soil temperature at hand, it was necessary to fall back on the temperature excess curve of Figure 4 for a correction to be applied to the mean air temperature. To obtain this temperature correction, the area under the excess curve (degree-hours) for the period of observation was divided by the number of hours in the period. The mean air temperature for the period plus the correction determined the value used as the mean soil temperature, which in turn determined the value of E_w used. Thus, all variables in the Fitzgerald equation were accounted for, except for the conversion of the values of V (rate of evaporation) from inches per day to total grams per cm² for the period, W (gm/cm²).

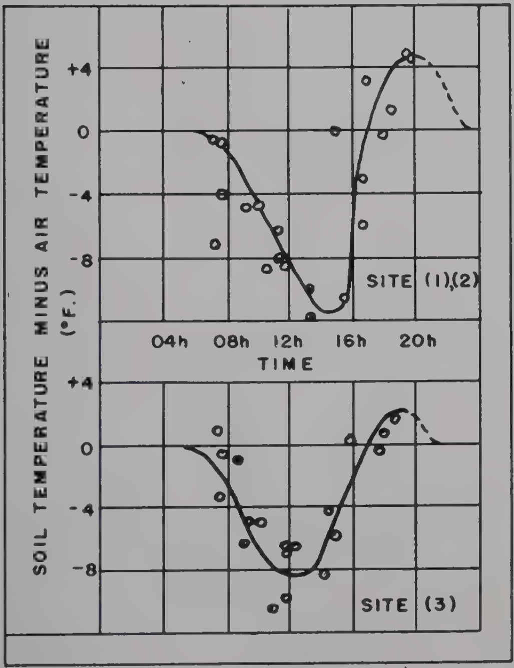


FIG. 4. Diurnal variation of (soil temperature minus air temperature).

The plot of calculated values against observed values for Site (1) (Fig. 5) shows the nighttime evaporation from the pan to be very well predicted by the method of calculation. True, the morning and night points (Table I) are slightly above the line of perfect correlation; but this may be accounted for by lower wind speeds than that assumed and by strong nighttime radiational cooling of the soil surface at high altitude, even under a copious canopy. The afternoon points lie on a line below perfect correlation, indicating an underestimation by the formula. Though the pan was in the shade during the day, this underestimation could be explained by the soil surface being warmer than that at a 3 cm depth and by higher wind speeds than assumed. It can be shown that the line of best fit passing through the scatter of afternoon points is that which would have resulted had a wind speed of 1.25 mph been assumed. This value (1.25 mph = 0.56 meters per second) agrees well with a value of 0.60 mps reported by Geiger (1950) for a similar pine stand. The dot-dash lines indicate the limits within which a calculated value would be within 50% of the observed value.

The plot for Site (2) (Fig. 6) shows considerable scatter and almost no stratification of data

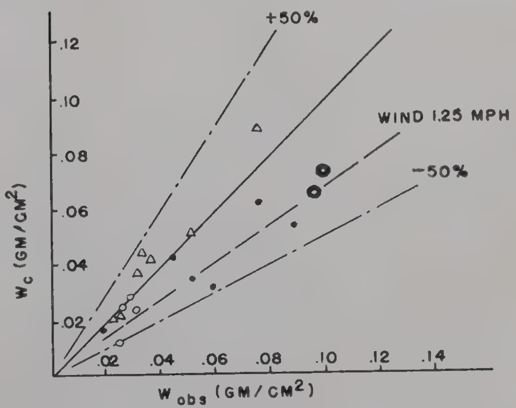


FIG. 5. Observed evaporation vs. calculated evaporation for Site (1) using Fitzgerald's formula.

TABLE I. Key to graphic symbols indicating time of day of observation period (all times Pacific Standard)

Observation period entirely within time 0600 - 1200	○
Observation period entirely within time 1200-1800	●
Observation period entirely within time 1800 - 0600	△
Observation period with at least 2 hours during 0600-1200 followed by at least 2 hours during 1200-1800	◉
Observation period with at least 2 hours during 1200-1800 followed by at least 2 hours during 1800-0600	◬
Observation period with at least 2 hours during 1800-0600 followed by at least 2 hours during 0600-1200	⊚
Observation period longer than 12 hours, regardless of time of day.	◘

according to time of day. This is probably to be expected because the data from which Fitzgerald first derived the formula were gathered with wind and temperature instruments very close to the water surface, as is the case with Site (1). However, the fact that there is no strong stratification (regardless of degree of correlation) seems to point to the idea that there is no great consistency in the relationship of the moisture gradient to the temperature gradient higher than the first foot or so above the site.

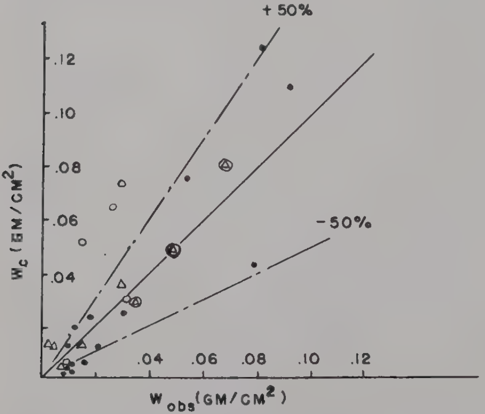


FIG. 6. Observed evaporation vs. calculated evaporation for Site (2) using Fitzgerald's formula.

The plot for Site (3) (Fig. 7) shows an immense overestimation by the formula. The curve to the left drawn by eye through the values as computed by Fitzgerald's formula suggests some sort of logarithmic function. Although no doubt not the best adjustment possible, the following equation linearizes the data sufficiently to justify saying that there is a logarithmic relation between the evaporation in a restricted site and that which one might expect at an open site under the same conditions:

$$V = .00873 \left[\ln \left\{ (0.40 + 0.199\, u) \cdot (E_w - E_a) \right\} + 5.188 \right]$$

Rohwer (1931) reports an empirical equation derived for use in still-air evaporation problems, but application of this equation to the data from Site (3) yields nothing in the way of a systematic relationship with the observed evaporation.

The most useful notions to come out of the use of Fitzgerald's formula might be that, 1) when the forest soil is still quite damp in the early summer, it can be expected to behave (with proper qualitative allowances for type of site) like a free water surface with respect to evaporation rates; and 2) many clues may be obtained by this comparison as to how the microclimate deviates from the microclimate of a site such as Fitzgerald used.

Using these same data in an equation of the form (3) gave results quite closely comparable to those of Kucera (*op. cit.*) (See Table II and Fig. 8). Thus, the basic concept of the vapor pressure deficit has been applied once again, this time to evaporation data from a subalpine environment with results equally as convincing as those from other environments from quite different climatic areas.

TABLE II. Correlation coefficients for various evaporation approximation methods as applied to data from Donner Summit, California

Method	Night and morning data	Afternoon data	All data
Fitzgerald's formula, Site (1)	....	....	0.85
Eq. (3), Vapor pressure deficit, Site (1)	0.88	0.38	0.92
Eq. (3), Vapor pressure deficit, Site (3)	....	....	0.75
Eq. (9), V.P.D. extension, Site (1)	....	....	0.74
Eq. (10), "P" method, Site (1)	0.88	0.67	0.88
Eq. (10), "P" method, Site (3)	....	....	0.87
Eq. (10), "P" method, Site (4)	....	....	0.97

AN EXTENSION OF THE VAPOR PRESSURE DEFICIT IDEA

Let us assume equation (3) to be correct and rewrite it slightly:

$$\frac{dW}{dt} = A\,(E_s - E) \qquad (4)$$

W = evaporation in gm/cm^2

A = constant = .773 in the case of Site (1) (Fig. 8)

E_s = saturation vapor pressure of the air (mb)

E = ambient vapor pressure of the air (mb)

t = time

Since the relative humidity is defined as the ratio

$$r = E/E_s$$

we may rewrite the evaporation equation (4)

$$\frac{dW}{dt} = A\,(1 - r)\,E_s$$

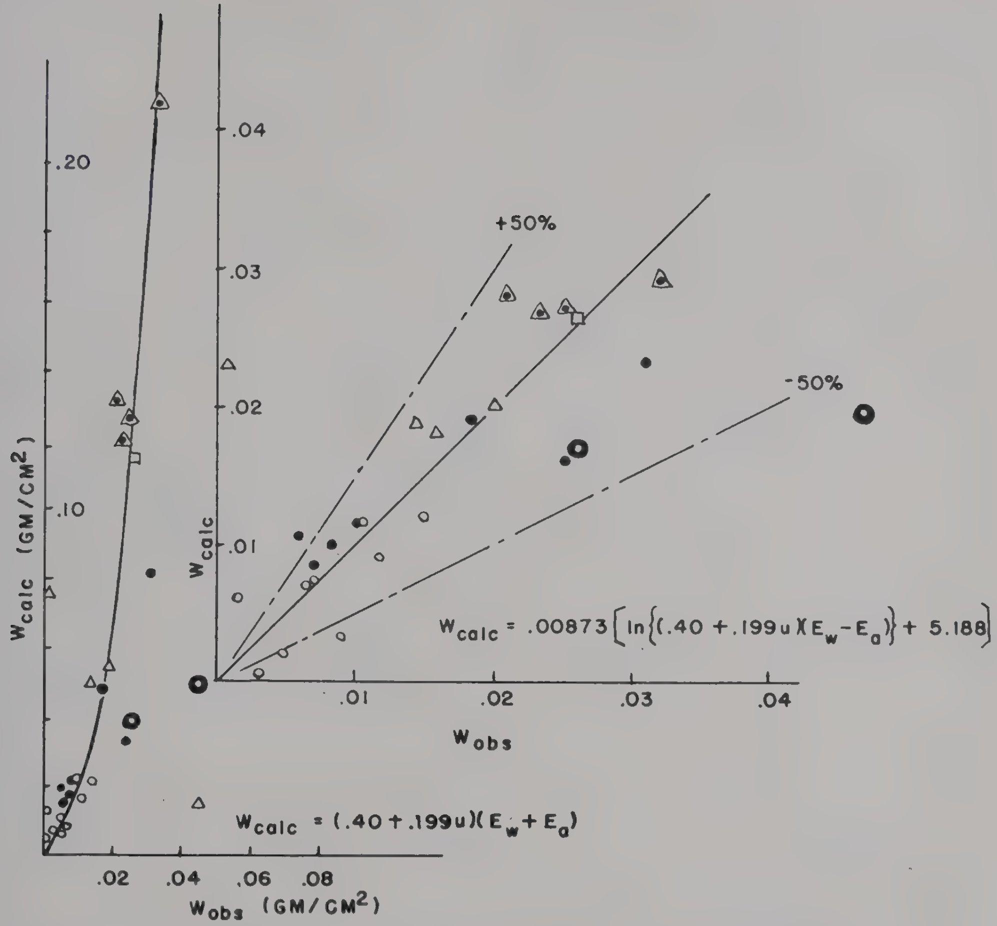


FIG. 7. Observed evaporation vs. calculated evaporation for Site (3) using Fitzgerald's formula.

and if we define R = (1 — r), we have

$$\frac{dW}{dt} = ARE_s \qquad (5)$$

Now thermodynamic theory states that saturation vapor pressure over water is a function of absolute temperature alone: (in terms of natural logarithms) (Holmboe *et al.* 1945: 51)

$$E_s = e^{-(B/T) + C}$$

for example: $B = 5418$; $C = 19.336$
when: E_s in centibars
T in absolute temperature (°K).

Since the temperature and relative humidity may be expressed as certain functions of time through a diurnal cycle:

$$T = F_1(t) \qquad R = F_2(t)$$

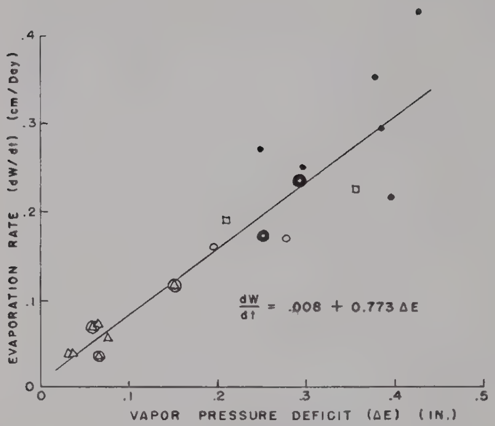
we are in a position to express evaporation as a function of time alone:

$$\frac{dW}{dt} = A \cdot F_2(t) \cdot e^{\left(\frac{-B}{F_1(t)} + c\right)} \qquad (6)$$

Equation (6) is an ordinary differential equation of W in terms of t. Perhaps if we knew F_1 and F_2 we could integrate and know W explicitly. But the first problem now is to find (or approximate) F_1 and F_2. For a day or group of days having maximum temperature (T_M) and minimum temperature (T_m), maximum relative humidity (r_M) and minimum relative humidity (r_m), F_1 and F_2 might be approximated roughly by very simple periodic functions:

$$T = \left(\frac{T_M - T_m}{2}\right) - \left(\frac{T_M - T_m}{2}\right) \cdot \mathrm{Cos}\, 2\pi t \approx F_1(t) \qquad (7)$$

$$R = \left(\frac{(1 - r_m) + (1 - r_M)}{2}\right) - \left(\frac{(1 - r_m) - (1 - r_M)}{2}\right) \cdot \cos 2\pi t \approx F_2(t) \qquad (8)$$



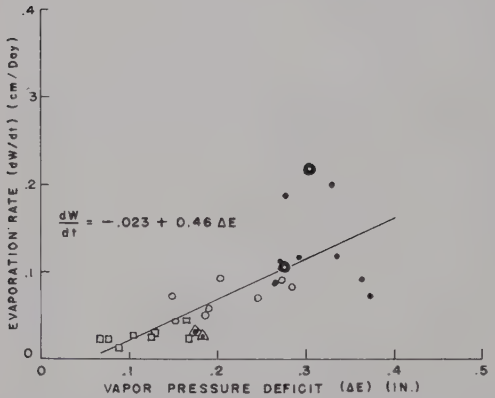


FIG. 8a. Vapor pressure deficit vs. evaporation rate for Site (1).

FIG. 8b. Vapor pressure deficit vs. evaporation rate for Site (3).

when $t = 0$ is perhaps 1 A.M. and $t = 1$ is 24 hours later (see Fig. 9). So now, to approximate the instantaneous rate of evaporation at time t, all we need to know is T_M, T_m, r_M, r_m and three constants A, B, C, according to equations (6), (7), and (8).

If the mean temperature is $\bar{T}$, the departures of T_M and T_m from $\bar{T}$ equal T′, and similarly for R and r, equation (6) becomes.

$$\frac{dW}{dt} = A\,(\bar{R} - R'\cos 2\pi t)\, e^{-[B/(\bar{T} - 2T'\cos 2\pi t)] + c} \qquad (9)$$

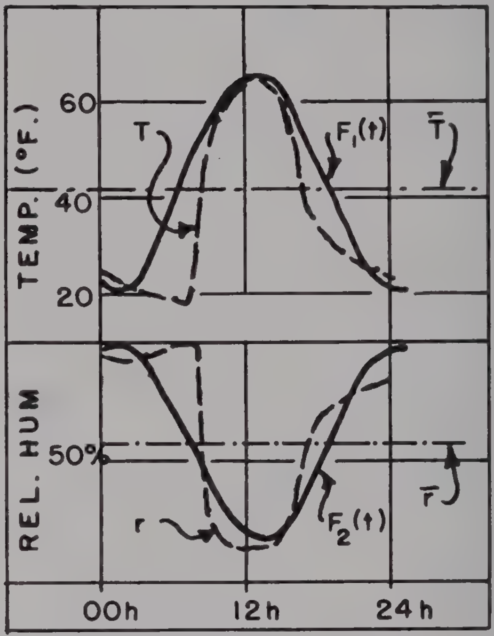


FIG. 9. Illustrating how simple periodic functions approximate R and T.

To solve this differential equation for total evaporation W appears quite formidable. But since there is only one independent variable, it might be possible to solve for dW/dt for various values of t. We would then have the slope of the W vs. t curve for the several values of t, and a good approximation to the integral curve may be drawn by simple geometric construction using these slopes. But the problem then arises to construct a scale of W on the graph to go with the curve and the scale of t. One value of W can be computed consistent with the preceding approximations as follows:

Using equations (7), (8), and then (9) and setting $t = \frac{1}{4}$, $dt = \Delta t = 1$ (day), we may calculate $dW = \Delta W$ for one day:

$$\Delta W = A\bar{R}e^{-(B/\bar{T}) + C}\Delta t = A\bar{R}\bar{E},$$

where $\bar{E}$ = mean daily vapor pressure, and A is evaluated from (3). Now we have two points on our scale of W: $W = 0$ for $t = 0$, and $W = \Delta W$ for $t = 1$. Making a linear scale for W to conform to these two points completes the construction of the W vs. t curve (see Figure 10). Assuming our approximations for R and T are satisfactory over a period of time, say a week, we may approximate the total amount of evaporation from the curve of equation (9) simply by the change in W from the beginning of our sample period to the end. For example, if a sample period began at 0800 on D-day and ran until 1600 on D + 3-day, we would first read the value

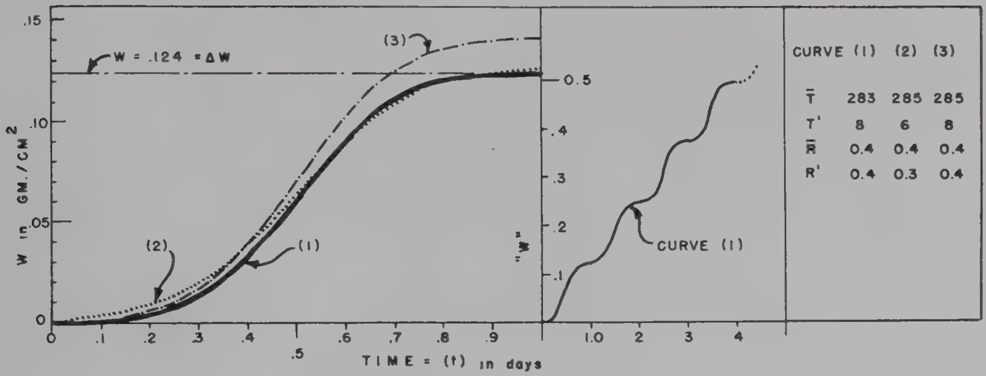


Fig. 10. Evaporation vs. time with variations in $\bar{T}$, T', $\bar{R}$, R', according to Equation (9).

of W above $t = 0.33$ $(= 8/24)$ and then subtract it from the value of W above $t = 3.67$ $(= 3 + 16/24)$ to get the total evaporation in the period. Some idea of the variation of equation (9) with variations in $\bar{T}$, T', $\bar{R}$, and R' may be gotten from the secondary plots in Figure 10. The equation is examined merely to suggest how mathematical statements of the variation of evaporation through the day may be developed.

The application of this extension of the vapor pressure deficit idea to the data from Site (1) gives results having quite acceptable reliability when compared with those relationships of the form of equation (3). Obviously, the better the mathematical approximations used in (7) and (8), the better will be the results from (9).

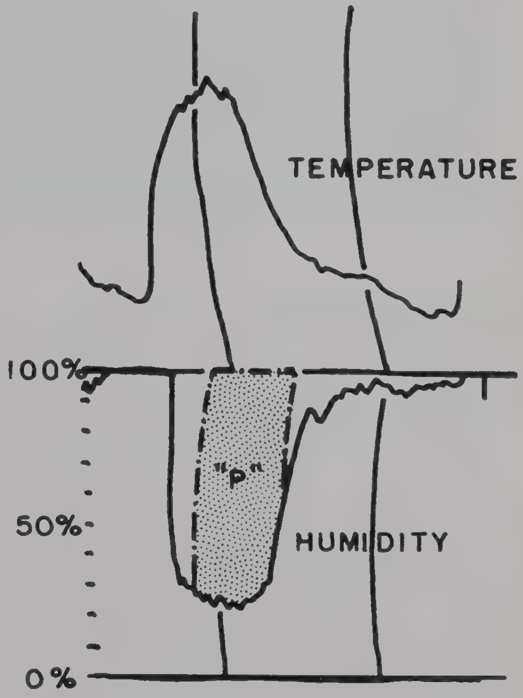


Fig. 11. Illustrating area "P" on a hygrograph chart.

A Further Extension

A close look at equation (9) suggests a further extension of this approach. Since T is expressed in degrees Absolute (that is freezing = 273° A.), the percentage change in T through the day is relatively small: *i.e.,* $T'/\bar{T} \approx 3.5\%$ only Because of this, we may consider $\bar{T}$ to be a constant temperature through the day, with a resulting constant saturation vapor pressure, $\bar{E}$. Equation (5) then becomes:

$$\frac{dW}{dt} = A\bar{E}R = (A\bar{E}) \cdot F_2(t) \text{ and } dW = (A\bar{E})\, Rdt.$$

Intergrating the expression now between limits:

$$\int_0^w dW = (AE) \cdot \int_0^t Rdt \qquad (10)$$

gives us a new expression $W = A\bar{E}P$ when we define $P = \int_0^t R\, dt$. For a given observation period during which a continuous record of relative humidity (and thus, R) was obtained on a hygrograph chart, P is represented by the area on the chart between the trace of relative humidity, the 100% humidity line, and the beginning and end of the period (see Figure 11). Since $(A\bar{E})$ is very likely almost constant for a given environment, or surface, for a period of possibly a week or so, an observer may "calibrate" an area for quick approximations of evaporation.

To make this calibration, simply obtain several measurements of evaporation (*e.g.,* as described above using pan and scales) along with a humidity record. Then, planimeter, or measure the area, under the trace on the chart for each sample period. This area, P, when plotted against the

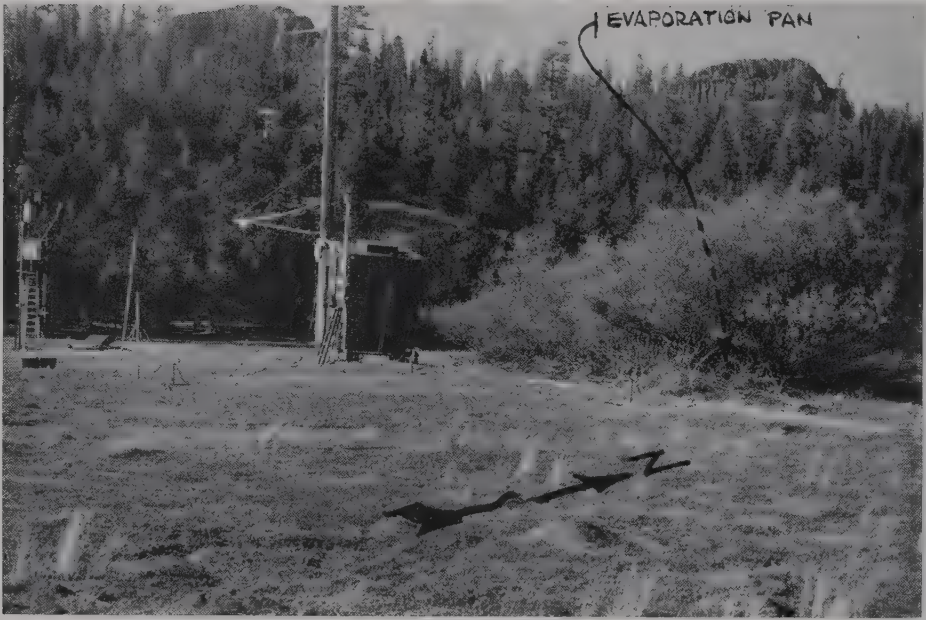


FIG. 12. Site (4) looking northwest.

observed W on log-log graph paper should give a straight line with slope 1 by the nature of equation (10).

Examples of such plots for the three sites of the Donner Summit study and an additional Site (4) in a subalpine meadow (Figure 12) appear as Figures 13, 14, 15, and 16. Of particular interest is the fact that in Sites (1) and (2), where the pan was open to vigorous wind action and strong diurnal heating nearby, the afternoon points lie along a distinctly separate line with slope greater than 1. In Sites (3) and (4) this apparently does not happen, and the slopes are very nearly 1. Values of "P" are expressed as fractions of the total area between 100%, 0%, and two time lines one day apart, *i.e.,* the maximum possible value of "P" for one day. Note the scale in the figures is 245 P, since the planimeter used measured 245 units for this maximum daily area for "P."

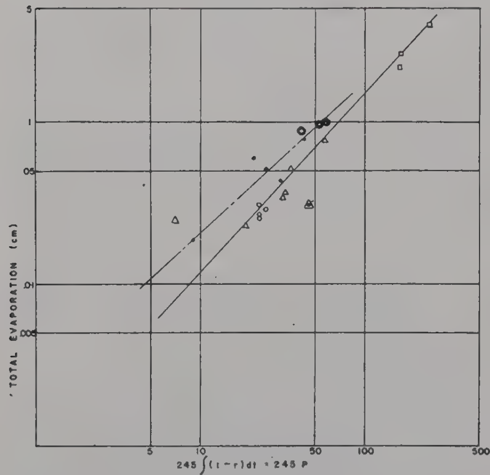


FIG. 13. Estimation of total evaporation by the "P" Method, Site (1).

Correlation analyses of these plots (Table II) show that the predictability of evaporation using this method is consistently as high as by the two standard methods mentioned, if not higher. When combined with the reduced expenditure of work in calculation and elimination of the use of tables of vapor pressure, this feature of high predictability makes the planimeter, or "P" Method, seem worthy of consideration as a field method for approximating evaporation. In addition, the method results in an estimate of evaporation directly and not of an evaporation rate for the observation period.

The principal limitations of the method appear to be:

1) the tacit assumption of a uniformly cyclic environment as regards air temperature and wind for the estimation period,

2) assumption of constant supply of soil moisture in the surface layer through the estimation period,
3) no allowance for dewfall,
4) the length of continuous estimation period during which the method is usable depends on site, climatic area, and probably season.

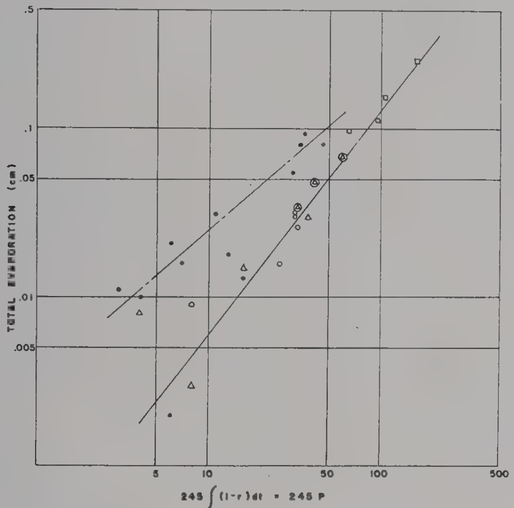


FIG. 14. Estimation of total evaporation by the "P" Method, Site (2).

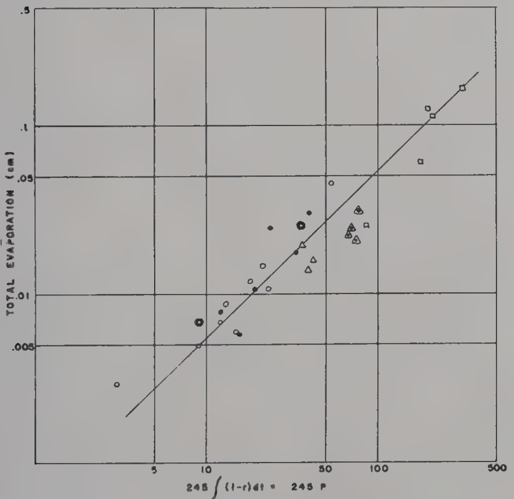


FIG. 15. Estimation of total evaporation by the "P" Method, Site (3).

Much work on the applicability of this "P" Method to widely varying environments could be done with very small investments of time and instruments. Two suggestions to further reduce the time involved in getting a field approximation by this method follow from the nature of equation (10) and the nature of the trace on the hygrograph chart:

1) Diurnal variations in evaporation rate are damped out when an observation period extends to about 3 days, as shown by the fact that the two lines converge to the right in Figures 13 and 14. Therefore, the evaluation of equation (10) could theoretically be accomplished by setting out a weighed evaporation pan and then weighing it again 3 to 5 days later. The total area P obtained and the W measured for this period would determine a single point on the log-log graph. If a line with slope 1 were then drawn through this point, the approximating curve would be complete.

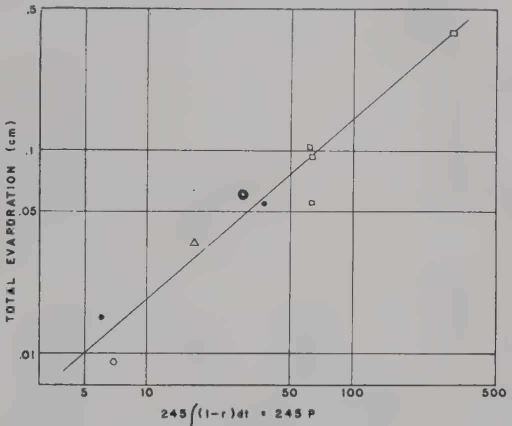


FIG. 16. Estimation of total evaporation by the "P" Method, Site (4).

2) Instead of using a mechanical planimeter to measure the area under the humidity curve, one could use an overlay with small grid or the chart itself, and just count squares (and half-squares) to get a relative measure of the area.

Summary

Two standard field methods for approximating evaporation (rates) based on the vapor pressure deficit concept have been reviewed and applied to data collected in several kinds of environments near Donner Summit, California. The reliability of the methods at high altitudes compares well with results reported by other workers in other areas.

A mathematical extension of the vapor pressure deficit equation is developed, leading to a much simplified method of making field approximations. If a soil-filled pan is placed level with the soil surface and weighed periodically to obtain a measure of evaporation, and a hygrograph giving a continuous humidity record is placed beside the pan, it is shown that the area under the humidity trace on the chart and between the beginning and ending times of the observation period yields a straight line relationship when plotted on log-log graph paper against the evaporation measured for the same period.

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GERMINATION REGULATING MECHANISMS IN SOME DESERT SEEDS

III. *CALLIGONUM COMOSUM* L'HER.[1]

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Introductory

Calligonum comosum is a summer-shedding woody shrub, reaching a height of 100-120 cm., and a crown diameter of 100-350 cm. The plant is a native of coarse sandy soils in the Sahara (Good 1947) and in the Negev (southern Israel; Eig, *et al.* 1948). Together with *Haloxylon persicum*, it forms the climax vegetation in the sandy soils of the borders between the Saharo-Sindian deserts and the Irano-Turanian steppes, where annual precipitation does not execed 150 mm. The plant is considered as a valuable perennial pasture plant for the above-mentioned regions (Boyko 1949a), and an excellent binder of shifting sands, owing to its high resistance to sanding-over (author's observations).

The dispersal unit is a brownish-red achne, covered from tip to tip with 8-16 rows of bristles. The achene itself is 10 mm long and 3-4 mm thick, but with the bristles, it reaches a length of 20-25 mm and a thickness of 15-20 mm. The bristles are soft and elastic, and break off quite easily. They do not attach themselves to wool, etc., but appear to serve in fruit dispersal by helping the fruits to roll along the ground under the influence of winds, through the springy nature of the bristles.

The fruit coat is about 1 mm thick and very tough. It was found impossible to remove the fruit coat without damaging the seed, and consequently all germination tests were carried out with intact dispersal units.

Materials and Methods

The dispersal units were collected in Nahal Timna (Wadi Menaiyeh) in the southern Negev, in May, 1951. Germination was carried out on filter paper, cotton wool, or coarse sand in Petri dishes; or imbedded in coarse sand, inside deep plastic containers. Tap water was used throughout. Counts were usually started after four or five days, and repeated at two-day intervals. Illuminated incubators at 15°, 20°, 26°, and 30°C. were used. Most experiments were run parallel in continuous light and in dark (obtained by placing the dishes or containers inside light-tight tins).

Results and Discussion

(1) Light and temperature effects

The effects of various light/temperature combinations on germination of the dispersal units

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[1] Thanks are due to the Ford Foundation which supported this work. The author wishes also to express his thanks to Professor Michael Evenari for his kind interest throughout this work, and to Messrs. Moshe Negbi, Yehuda Ben-Shaul, and Dan Cohen for their assistance in the field experiments.

TABLE I. Germination of dispersal units of *Calligonum comosum* under various light/temperature conditions. Average percentages on seventh day of seven separate determinations (only 5 at 30°C.) between March and November, 1953, 25 or 50 fruits per sample

Temperature (°C.)	LIGHT		DARK	
	% germination	Standard deviation	% germination	Stqndard deviation
20°.........	14.6±4.1	10.93	71.1±2.7	7.10
26°.........	4.0±1.7	4.47	59.4±7.1	18.67
30°.........	0.4±0.4	0.89	12.0±5.9	13.27

were tested numerous times between March and November, 1953. No germination occurred at 15°C. The results of the tests between 20 and 30°C. are presented in Table I.

From these results, it appears that germination of dispersal units of *Calligonum comosum* takes place between 20 and 26°C., and that low (15°C.) and high (30°C.) temperatures are unfavourable. It is also clear that light inhibits germination at all temperatures, but that its action is, to some degree, modified by the lower germination temperatures. Inspection of the standard deviations presented in Table I shows that, in several cases, the variability of the results was rather large. As the dispersal units were often infected by a fungus with large black sporangia on the tips of the bristles, it was thought that this fungal infection might be responsible for the variability of the results. It was, therefore, decided to reduce this infection by treating the seeds with fungicides.

(2) Sterilization tests

Lots of 50 dispersal units each were vigorously shaken with 1 per cent (by volume) bromine water for 1 minute, and then rinsed 10 times in 100 ml tap water. Dispersal units thus treated germinated 14, 16, and 4 per cent respectively, within 6 days, when sown at 20°, 26° and 30°C. Since all dispersal units were entirely free of infection, it seemed likely that the bromine was harmful to the embryo, and was responsible for the inhibited germination. It was, therefore, decided to try the effects of $HgCl_2$.

Lots of 50 units each were vigorously shaken in a 1 per cent $HgCl_2$ solution for 1, 2, and 5 minutes respectively, then rinsed thoroughly by shaking 5 times with 100 ml tap water. Controls were shaken in tap water for 5 minutes, then washed as above. Germination was carried out at 26°C. in the dark. Not a single seedling had germinated from the treated units within 9 days, though they were entirely free from infection. Also, not a single seedling had germinated from the controls, though they too were entirely free from infection.

One conclusion to be drawn from the above experiments is that the fungus is plant-borne, and easily washed away by shaking with water. Another conclusion is, that the short shaking with water (5 to 10 minutes) was sufficient to cause complete inhibition of germination. This aspect was further investigated.

(3) Washing effects

One possibility for the total inhibition of germination caused by washing the units is that, during the water treatment, light starts to act on the moist units, and causes their inhibition. That this is unlikely is shown by the fact that even in light there is some germination. However, the possibility was investigated.

Duplicate lots of 20 units each were shaken during half an hour in 10 portions of 100 ml. water each. Water temperature was 25°C. One treatment was carried out in full daylight, another treatment was carried out in total darkness. After treatment, the units were sown in 26°C. in the dark. Duplicate lots of untreated units were sown under the same conditions. Great care was taken that the units treated in darkness would not be exposed to light at all until the (single) final count was made 6 days later. Not a single seedling had germinated from any of the treated units, but the controls germinated 60 per cent.

The washing treatment may interfere with germination in several ways. One possibility is that, during the washing, essential substances are leached away from the fruit. Another possibility is that the treatment causes the blocking of air inlets into the embryo by water. It was, therefore, attempted to give the leaching effect, without blocking of the air inlets by water at the same time. Two lots of 50 units each were vigorously shaken with 10 portions of water, 100 ml. each, during a total of 30 minutes. Then 25 units from each lot were sown at 20°C. in the dark, and the rest dried for 7 hours in a desiccator over $CaCl_2$, and later sown under the above conditions. Duplicate lots of 25 untreated units each were sown under the same conditions, as controls. Within 5 days, germination of the controls had reached 70±6 per cent. Washed units had not germinated at all, while the washed and dried units had reached 28±0 per cent. After a further 7 days, germination of the controls had reached 72±8 per cent, the washed units had still not germinated, while the washed and dried units had reached 42±2 per cent.

From these results, it appears that though washing itself inhibits germination completely, drying after the washing restores germinability. On the other hand, drying did not restore germinability completely, as is evident from the low rate of germination of the washed and dried units, and from their comparatively low final germination percentage. At this point, it may be assumed that the "washing effect" has an inhibitory effect on germination through the blocking of the air passages in the fruit, but that it also has another, as yet unexplained, inhibitory action.

Ecologically, this "hydrophobic" germination has interesting implications. The limits of distribution of this species are, ecologically, rather well-defined, and confined to coarse sandy soil in regions where annual precipitation, though low in amount, nevertheless varies within narrow limits. Inhibitory action of large amounts of rainfall on germination may be one of the decisive factors which delimit the ecological distribution of the species to areas of low rainfall. The inhibitory action of light upon germination may also be interpreted as a modification of high survival value for a species inhabiting arid deserts, where moisture conditions on top of the soil are extremely uncertain. Conditions under the soil surface are much more favourable, in particular in sandy soil, where water is efficiently protected from evaporation by the low capillarity of the dry sand cover (Zohary 1944: 167). In this respect, the bristly construction of the fruit takes on an added significance, because in the coarse sandy soils, to which this plant is confined, the bristles serve to create a soil-free cavity around the fruit, thereby preventing a close contact with water.

(4) Light effects

Germination of *Calligonum comosum* is light-sensitive (Table I). The fruit coat is, however, quite thick, and as far as could be ascertained without direct measurement, impenetrable by light. This raised the question as to the ability of the embryo to react to light which, apparently, does not reach it. The only possible contact with light is the narrow perforation in the micropylar end of the achene (this perforation is so narrow that it is hardly discernible). In order to check this possibility, the following experiments were set up:

Four deep dishes were filled with moist coarse sand. Twenty holes were bored in the sand in each dish, by means of a glass rod, to a depth of 10 mm. Into the holes in 2 of the dishes, fruits of *C. comosum* were inserted vertically with the perforated end up, so that only 1 mm of the fruit projected above the soil. In the 2 other dishes, fruits were likewise inserted, but with the perforated end down. The dishes were transferred to 20°C. and left in the light. On the fourth day, it was found that while fruits planted with perforated end down germinated 60±10 per cent, the others had germinated only 17.5±2.5 per cent.

The marked inhibition caused by planting the units with their perforated end above the soil could arise from the following causes: (a) gravitational effects hindering the positively geotropic radicle from the growing in the inverted position; (b) insufficient hydration of the embryo, when the easiest water inlet lies outside the soil; (c) the locus of light perception in the embryo is in the region of the root-tip (which lies nearest to the perforation).

In order to differentiate between the various possibilities, the above experiment was repeated (duplicate lots of 25 fruits each per test), this time in both light and dark. Germination percentages on the fifth day are presented in Table II.

Table II. Localisation of region of light-perception in fruits of *Calligonum comosum*
(Explanations in text)

	Perforated End of Fruit	
	Up (outside soil)	Down (inside soil)
Light	36 ± 4	84 ± 0
Dark	76 ± 12	70 ± 2

From these results, it is evident that whereas in darkness the orientation of the perforated end had no effect on germination, in the light the germination of those fruits whose perforated end projected from the soil was markedly inhibited. It is worthy of mention that in both the above-mentioned experiments radicle growth was inhibited only when the perforated end was exposed to light.

These results indicate that the third of the above-mentioned possibilities is the most plausible, and that the light-inhibited germination in this species is due to perception of the light stimulus in the root-tip region of the embryo, through the small perforation in the micropylar end of the fruit.

(5) Field experiments

With consideration to the observed data, it was decided that the reseeding of the depleted desert pastures in sandy soils with this species was quite feasible. All that was needed was the selection of the right season for temperature, and deep planting of the fruits. This was accordingly tried.

After a rain in the early spring of 1955, a few rows of fruits were planted in depressions in different localities in the Tureibe plain in the Negev. Depth of planting was approximately 10 cm. Although the sand was still moist from the rain, very small amounts of water were used to irrigate the rows after planting, in order to restore the normal structure of the sand, which had been disturbed by the planting. Very good emergence was obtained almost in all localities, reaching 50 to 60 per cent, which is nearly equal to the germination percentages obtained in the laboratory. The plots were examined at later dates, and it was observed that wherever the structure of the sand had not been disturbed by the flocks belonging to desert nomads, and the seedlings uneaten, seedling establishment was quite high. However, whether the plants are really established or not, is a question which will have to wait at least another year of observation for its answer.

CONCLUSIONS

Germination of *C. comosum* is inhibited by light, by high temperatures, and by close contact with water. This complex mechanism may be the one responsible for the confining of the germination, and hence also the distribution, of this species to coarse sandy soil in areas of low rainfall, which are indeed the conditions found in its natural habitat.

Under natural conditions, it seems that there are two factors which limit the propagation of this species. One is the difficulty with which its fruits may achieve deep penetration into the sand (which is apparently the only place where they can germinate under field conditions). In this connection, the remarks made by Boyko (1949b) on the decisive importance of minor modifications in the germination bed, such as small holes made by burrowing animals and insects, are very significant. The other factor which limits distribution is the rarity of occasions when sufficient rainfall conicides with the proper germination temperatures.

Range reseeding with this species was found to be quite feasible with relatively low expenses. It is too soon to know, however, the percentage of successful establishment of mature plants.

SUMMARY

1. Germination of fruits of *Calligonum comosum* was found to be inhibited by light and by higher temperatures.

2. A vigorous shaking in water during less than 30 minutes completely inhibited subsequent germination. Drying such washed fruits did restore germinability, but to a lesser degree.

3. The site of light-perception has been localised in that part of the embryo nearest to the micropyle.

4. Successful reseeding of depleted desert pastures with this species has been carried out.

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THE COMMUNITIES OF ALGAE IN THE SPRINGS AND SPRING STREAMS OF FLORIDA[1]

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A combination of climate and geological features have produced, in the State of Florida, a series of aquatic habitats unique in the Southeast, if not in the world. These are the giant springs and spring streams, 17 of which have a flow of more than 100 second-feet (3 cu. m. per sec.), and 49, a flow of 10 to 100 second-feet (0.3 to 3 cu. m. per sec.). Many of the springs have large open pools, and the runs or streams from them flow for many miles with almost no contamination by surface water. Thermal and chemical conditions are remarkably stable so that the only important habitat variable is light. Basic data on the chemical and physical characteristics of these springs can be found in Ferguson, *et al.* (1947), and further data, as well as productivity studies, in reports by Odum (1953).

Relatively little is known of the algal flora of streams in the Southeast, and apparently, no

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studies of the flora of such springs have been published in this country. Beginning with the classic papers of Kofoid (1903, 1908) on the Illinois River, occasional papers on stream limnology have appeared, but the plankton has received almost all of the attention. Some of these papers are those of Galtsoff (1924), Reinhard (1931), and Chandler (1937). Shelford and Eddy (1929) suggested methods for long-time studies of stream communities. Eddy (1925) reported a brief study of a small stream in Illinois. Most other limnological studies or surveys have dealt with animals or higher aquatic plants with almost complete disregard for the algae, especially of rapid streams.

In Europe somewhat more work has been done, Limanowska (1912) investigated a short stretch of the Limmat, Budde (1928) and Thienemann (1931) a series of springs and brooks, Fritsch (1929) and Godward (1934) the algal communities of streams, and Pearsall and Schroeder (1930) surveyed the River Wharf. A series of papers, chiefly by R. W. Butcher, have made the algal flora of English rivers well-known, Butcher (1932, 1940, 1942, 1946). His 1946 paper is especially significant. He points out that there is no seasonal variation in the dominant species, that there is a greater abundance of algae in rapid streams, and emphasizes the importance of the water "being continually renewed over the algal surface." Ruttner (Frey and Fry translation 1952) expresses this idea even better in a negative way. He says, "In quiet or weakly agitated water the organisms are surrounded by a closely adhering film of liquid, which speedily forms around the plant or animal a cloak impoverished of substances important for life." The importance of attached algae in streams has come to be recognized, and the fact that many species, reported as plankton in earlier papers, actually are derived from communities of sessile algae and are not true plankton organisms.

Two pertinent papers are those of Budde (1932) and Hohn (1951) which report algae from saline inland waters.

As mentioned above, the volume of flow of the different springs varies greatly but in a single spring it varies only about 20 per cent annually. Temperature variation is less than 1°C annually in many springs and only slightly more down run. The temperature of the large springs is as low as 21°C in the northern and western part of the state and as high as 25°C in the south (Warm Salt Springs is 30°C). The gas and mineral content are invariable from day to day. Light intensities are generally high throughout the year except for a variable period of cloudy weather in winter. Day length is about 4 hours shorter in December than June. Since the only important habitat variable is light, data on insolation and light penetration are important. Such data, however, are not available for most springs. Secchi disk readings show the water to be remarkably clear. The disk can be clearly seen at the bottom of springs 15 meters deep and horizontally at 105 meters. H. T. Odum has begun light penetration studies with a Western photronic cell and he finds that on a clear day in December, in Silver Springs, there is an average of 50 per cent light penetration at 2.5 m for 7 hours of the day. One is quite turbid (Warm Salt; Secchi-disk reading 1 ft.).

Except for a few springs in the western part of the state, which are not included in this study, the waters are hard, although there is considerable variation in mineral content from spring to spring. Several are oligohaline to mesohaline. One has half the salinity of sea water, and several are high in sulfates and hydrogen sulfide. Calcium is high, (30-70 ppm) except in the few soft-water springs, and nitrates are moderate (.04-0.5 ppm). Recent analyses by H. T. Odum (1953) and others, indicate that phosphorus is also moderate (.01-.17 ppm inorganic P). Chlorides, sodium, and potassium are high in the saline springs.

As to mineral content, 5, or possibly, 6 types of springs should be recognized: (1) soft, fresh-water, (2) hard, fresh-water, (3) oligohaline[2] (chlorides up to 600 ppm), (4) mesohaline (chlorides up to 9,000 ppm), (5) sulfide, and probably (6) salt, sulfide.

Collections made over a period of 3½ years from 30 springs have been examined. Six springs, representing 4 of the above types were studied intensively. Some 75 collections were made during 1951 and 1952 by H. T. Odum, J. H. Davis, and W. C. Sloan, of the University of Florida. During the summer of 1953, the writer made nearly 350 collections in 26 springs, and H. T. Odum added a dozen winter collections in early 1954. The writer's collections were made by systematic sampling across pools, vents or boils, and runs. Collections in 4 runs were made from the spring to where the run entered a larger stream or the Gulf, and in all cases several stations down run were established. In the pool and boil, samples were taken by wading and swimming with a face mask to a depth of 3 m.; in the run, by wading and diving from a boat, in deep boils (up to 15 m.) with an Ekman dredge and water telescope for observation. Leaves of flowering aquatics of

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[2] The scheme of Redecke (1922) for the classification of estuarine waters seems to be reflected in the distribution af algae in the saline springs and the Gulf estuaries, therefore it is used in this paper.

TABLE I. The numbered species in each community are the dominants. Together, they constitute an estimated 80% or more of the algal flora. b = boil or vent; p = spring pool; r = run or spring stream; pe = pool edge; rg = run near Gulf of Mexico

	1 Hard, fresh-water	2 Oligo-haline	3 Meso-haline	4 Sulfur	5 Warm salt
Bacillariophyceae					
Achnanthes exigua Grun.					pr
Achnanthes lanceolata var. elliptica Cleve	5bp	bp	pr	r	
Amphiprora pulchra W. Smith					pr
Amphora coffaeformis Ag.			bp		pr
Amphora proteus Greg.					p
Amphora veneta Grun.					2bpr
Biddulphia laevis Ehr.	r	bpr	bpr		
Biddulphia polymorphus Ehr.					r
Cocconeis pediculus Ehr.					pr
Cocconeis placentula Ehr.	1bp	1bp	1bpr	r	
Cyclotella meneghiniana Keutz.		bpr	bpr		
Cymbella mexicana (Ehr.) A.S.	bp	bp			
Epithemia musculus Keutz.			bp		r
Epithemia zebra (Ehr.) Keutz.		bp			
Epithemia sp.					r
Eunotia pectinalis (Keutz). Rabh.	b	r		r	
Fragilaria construens (Ehr.) Grunow	bp	r	r		
Gomphonema longiceps Ehr.	b	4bpr	bp	r	
Gomphonema sphaerophorum Ehr.	3bp		r		
Lichmophora flabellata S.B.D.			4bpr		
Mastigloia smithii Thwaites					r
Melosira borreri Grev.			bpr		r
Melosira granulata (Ehr.) Ralphs.	bp	r			
Melosira varians Ag.	b				
Navicula radiosa Keutz.			bp		p
Navicula sp.				bp	
Nitschia amphibia Grun.			r		
Nitschia filiformis (W. Smith) Husted			r		
Nitschia gandersheimensis Krasske					7pr
Nitschia linearis W. Smith					r
Nitschia macilenta Greg.					r
Nitschia paradoxa (Gmelin) Grun.		bpr	bpr		
Pleurosigma angulatum (Queckett) W. Smith			bp		r
Pleurosigma sp.		p			
Stauroneis sp.			p	r	
Stephanodiscus barkleyi Rattr.		bpr			
Surirella striatula Turpin			bp		
Synedra radians Keutz.			bp		
Synedra ulna (Nitsch.) Ehr.	b	bp		r	
Synedra ulna var. oxyrhynchus Hust.	2bp	3bpr		r	
Syndera sp.				bp	
Terpsinoe musica Ehr.	r	bpr			
Cyanophyceae					
Amphithrix sp.	b				
Anabaena sp.		r	p	r	
Aphanocapsa pulchra (Keutz.) Rab.					r
Aphanothece stagnina A. Br.					p
Aphanocapsa sp.				bp	p
Aphanothece nidulans P. Richt.					5p
Aphanothece sp.				r	
Borzia sp.			p		
Calothrix sp.	r			r	
Chamaesiphon sp.					r
Chroococcus limneticus Lemm.					p
Chroococcus turgidus (Keutz.) Naeg.			p	bp	pr
Gleocapsa gigas W. & G.S. West.				bp	
Lyngbya aestuari (Mert.) Liebm.		rg			
Lyngbya epiphytica Hieron.	b				
Lyngbya kutzingii Schmidle	b				r
Lyngbya martensia Menegh.			3bp		
Lyngbya nordgardhii Wille	p			r	
Lyngbya sp.				2bp	
Microcoleus chthonoplastes Thuret					r
Merismopedia elegans A. Br.			p		r
Nodularia sp.		r			
Oscillatoria princeps Vauch.				r	
Oscillatoria splendida Grev.	p				
Oscillatoria sp.			p	r	4bp
Phormidium autumnale (Ag.) Gomont				r	
Phormidium tenue (Menegh.) Gom.					p
Phormidium spp.				bpr	
Plectonema wollei Farlow	4bpr	bpr			
Spirulina gomontii Gutw.				b	
Spirulina nordstedtii Gom.					3bp
Spirulina platensis Geitl.					1bp
Spirulina subsalsa Oerst.				b	
Spirulina subtilissima Keutz.					r
Xenococcus sp.	bp				
Chlorophyceae					
Chara honemannii Wall					bp
Chara zeylanica Zaneveld	b				
Chara zeylanica fors. H. & J. Groves	r				
Cladophora sp. 1	bpr			r	
Cladophora sp. 2		2bpr			
Cladophora sp. 3					8r
Closterium	pe			r	
Entocladia sp.	b				
Enteromorpha plumosa Keutz.		5bpr	2bpr		
Eudorina elegans Ehr.		r			
Microspora floccuosa (Vauch.) Thuret	b				
Mougeotia sp.	r	r			
Oedogonium spp.	pr	bpr		r	
Pseudoulvella sp.	r			r	
Rhizoclonium fontanum Keutz.	p				
Rhizoclonium sp.	bpr			r	
Scenedesmus bijuga (Turp.) Lagerh.	pe				
Scenedesmus dimorphus (Turp.) Keutz.	pe		p		
Schizomeris liebleinii Keutz.	r			r	
Spirogyra sp.	bp	r		r	
Spirogyra sp. 2	p	r			
Spirogyra sp. 3	pe				
Stigeoclonium sp.	6bp		bp	r	
Xanthophyceae					
Vaucheria sp.	br				
Vaucheria sp. 2					r
Rhodophyceae					
Audouinella violacea (Keutz) Hamel	b				
Compsopogon coeruleus (Balbis) Mont.	r	bp			
Thorea ramosissima Bory	b				
Other Classes					
Euglena sp.	pe				r
Sargassum sp.		rg			

different ages were studied, as were "planted" glass microslides, and pieces of wood and plastic. Stone, sand, and ooze surfaces were sampled.

Collections were made on the assumption that there are three spring habitats namely, boil, pool, and run. This assumption was not warranted on the basis of the algal flora, as is pointed out below (Table I).

A No. 20 plankton net was used to catch drifting organisms and to check on the occurrence of plankton organisms. A few samples from springs and runs were kept in aquaria to see if phytoplankton would develop.

No exact quantitative studies were made but the numbers of organisms attaching to glass slides and to wood and plastic were determined for one spring. Scrapings, squeezings and concentrations of diatom material were dropped on cover slips and the protoplasm burned away on an electric hot plate. The cleaned valves were mounted *in situ* so that some idea of relative abundance of species could be determined as well as something of their relative abundance and position on the substratum. Systematic studies were made of small pieces of leaf and stem epidermis with the organisms in place. Tiny shavings of wood were examined in the same way and small groups of organisms scraped from stone surfaces were studied to determine relative abundance.

Attached algae make up by far the major portion of the algal flora in both spring and run. These organisms are attached largely to a few species of higher plants which are generally quite abundant in non-saline waters. Three species of flowering plants are the chief ones present. *Najas guadalupensis* is abundant especially in the boil or vent and the deeper portions of the pool, and in the run where not shaded by other species. It grows in fair abundance as deep as 10.5 m attached to both rock and soil. Epiphytes are not as abundant on this species as on the two others. *Sagittaria lorata* is next in abundance. It is most abundant in water under 3 m in depth. In the run, it may completely cover the bottom for long distances in a dense bed from 0.5 to 1 m deep. Not so widespread but very abundant in some runs is *Vallisneria neotropicalis*. It has leaves up to 4 cm wide and 1.5 m in length. Enormous beds, sometimes mixed with *Sagittaria* are found in several springs. Less abundant are several species of mosses which grow chiefly on rock surfaces apparently in waters with the highest oxygen content. Algae are sparse on mosses. Beds of *Chara*, a large green alga, are common in some springs. In the runs of Wakulla and Weekiwachee Springs, it is especially common and forms dense beds up to 0.6 m deep. Algae, especially diatoms, are abundant on *Chara*. *Ludwigia* sp. and *Hydrocotyle* sp. are abundant in the shallows of well-aerated pools. In one spring (Fanning), a species of *Polygonum* was fairly abundant in water 4.5 m deep! These species have relatively few epiphytes. The shallows of both pool and run support an assemblage of emergent flowering plants but their total under-water surface area is small compared with that of the species listed above.

Many diatoms and small blue-greens are epiphytic on the filaments of *Plectonema wollei* which forms large and abundant mats in the fresh-water springs. In the oligohaline and mesohaline springs, two species of *Enteromorpha* and *Potamogeton petcinatus* form important attachment surfaces for smaller organisms. All rock and wood surfaces are heavily encrusted with algae and in some of the smaller springs where water boils up slowly through beds of sand, diatoms cover the grains with a brown coat.

I. THE HARD, FRESH-WATER SPRING

Typical of the hard, fresh-water spring is Silver Springs, one of the largest springs in the world. The average flow of the principal boil is 940,000 cubic meters (250 million gallons) per day, and the total discharge of the 5 or 6 springs is twice this amount. The principal boil is a conical crater 10 m deep, and 20 m across at the rim. The water temperature is 23°C. The boil is near the center of a semi-circular pool 60 m in diameter and 3.6 m deep at the boil rim. The run, or spring stream, to the Oklawaha River is over 8 kilometers long and flows at the rate of 1 kilometer per hour. It varies from 20 to 30 m in width and from 2.5 to 5 m in extreme depth. Several smaller boils occur in bays or short side branches off the run. The bottom for the upper 3 miles is covered with thick beds of the aquatic plants listed above. The lower third is shaded by dense swamp forest and the aquatic plants with their encrusting algae are much less abundant.

Three complete series of samples were made in June, July, and August, 1953, and some samples collected at other seasons during the previous two years were examined. Glass micro-slides and strips of wood and plastic were "planted" for up to 3 months and removed at intervals for study.

By far the most important algal community is a lotic *aufwuchs*[3] in which 5 species of diatoms and one or possibly two species of blue-greens are the dominants. These are *Cocconeis placentula, Synedra ulna, Achnanthes lanceolata, Gomphonema longiceps, Gomphonema sphaerophorum, Amphithrix* sp. and probably *Plectonema wollei. Plectonema,* because of the large size of the plant masses and the fact that it is abundant on rock and soil in the boil, might be regarded as part of the next community but it seems to reach greatest abundance in the *aufwuchs* and should probably be placed there. *Cocconeis* is pioneer on most bare surfaces such as young plant leaves. It is followed by *Synedra, Xenococcus, Achnanthes,* and *Gomphonema.* These plants in turn are soon overgrown by other diatoms, filamentous green algae and *Plectonema. Amphithrix, Cocconeis,* and *Xenococcus* are most abundant in shady areas such as the deep boil, the under side of leaves and within plant beds. (Fig. 1.)

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[3] As pointed out by Frey and Fry (in the translation of Ruttner, 1952) the term *aufwuchs* is broader in connotation than periphyton. It seems more suitable here because it includes not only the microscopic organisms at-

In the pool and run, where there is a strong current, and especially near the surface, other species become more abundant among the dominants listed above. *Stigeoclonium, Oedogonium,* and *Cladophora* become attached among the dominant diatoms and other filamentous, but unattached, species such as *Rhizoclonium, Mougeotia, Spirogyra, Fragilaria,* and *Melosira* become part of the thick felted mass. Even a few single-celled or colonial species such as *Scenedesmus, Closterium,* and *Cymbella* are fairly common in the mats.

In heavily shaded areas such as lower Silver Springs run, the aquatic plants begin to drop out, the *aufwuchs* becomes sparse. Tufts of *Cladophora* and mats of *Vaucheria* in the shallows are the chief places where epiphytes can attach.

In the deep boil, *Chara zeylanica*[4] grows in scattered beds in which *Vaucheria* sp. and *Plectonema wollei* form large felted masses. The latter two species also colonize bare rocks and soil away from the *Chara* beds. *Thorea ramosissima* is common in algal felts here only. The *aufwuchs* described above is fairly abundant even here on the larger algae and on *Najas. Chara, Vaucheria,* and possibly *Plectonea* belong, I believe, to the rapids community of *Najas, Sagittaria,* and *Vallisneria* rather than to any algal community. This conclusion is borne out by observations in other springs where *Chara* and *Vaucheria* are much more abundant. In the runs of Weekiwachee and Ichatucknee Springs, *Chara* grows abundantly in the swiftest water and this seems true of the large felt-forming *Vaucheria.*

At the edge of the boil in very shallow water and among emergent aquatics, the typical lotic *aufwuchs* begins to be replaced by the littoral community typical of Florida ponds and lakes. Medium to large species of *Spirogyra* and *Oedogonium* are abundant and form floating mats in which *Rhizoclonium* and *Mougeotia* are also abundant. Also common are two species of *Scenedesmus,* and *Closterium* and *Euglena. Merismopedia* and filamentous blue-greens are common in the same situation in other springs. Lack of rapid current rather than difference in temperature or light conditions seems to be most important in preventing the typical spring dominants from being abundant here. The water is changed frequently enough that the temperature even in the afternoon of a bright summer day is only a few degrees above that in the boil, and obviously, the light is no brighter than on surface leaves of aquatics in the rapids of the run.

There is no true plankton in any spring and most of the runs. In the lower run of Homosassa where it becomes fairly slow and wide, plankton begins to develop and the same is true of the broad quiet estuary at Crystal River. Here five or six genera of plankton organisms were collected. That a plankton could develop in spring waters is proved by the presence of plankton species in spring water kept in aquaria for several weeks, and also by the rich plankton flora of nearby lakes with similar chemical composition.

The most important springs community, the *aufwuchs,* seems definitely a perennial vernal community. In fact there is no detectable change in dominance or species composition throughout the year in any of the spring's communities. There is a reduction in numbers of organisms during long periods of lower light intensity especially in winter. The writer's theory that shade species which grow deep in the boil in summer, migrate upward and out into the pool in winter does not seem to be borne out by observed facts.

Almost no work has been done on actual abundance of algae or on growth rates, but it seems certain that about half the total plant growth in the springs and their runs, is algae (Odum 1953 c, d).

Some study of the types of algae attaching to different surfaces has been made. On ooze and organic soils, only *Chara* and *Vaucheria* are important. There seems to be little difference in the species attaching to limestone, sandstone, and plant surfaces. On sand, several species of di-

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tached to free surfaces of underwater objects (periphyton) but also free-living organisms within the mats of attached species.

[4] The species of charads collected during this study were identified by Fay K. Dailey. Thanks are due her for this and also for checking my identification of *Thorea ramosissima.*

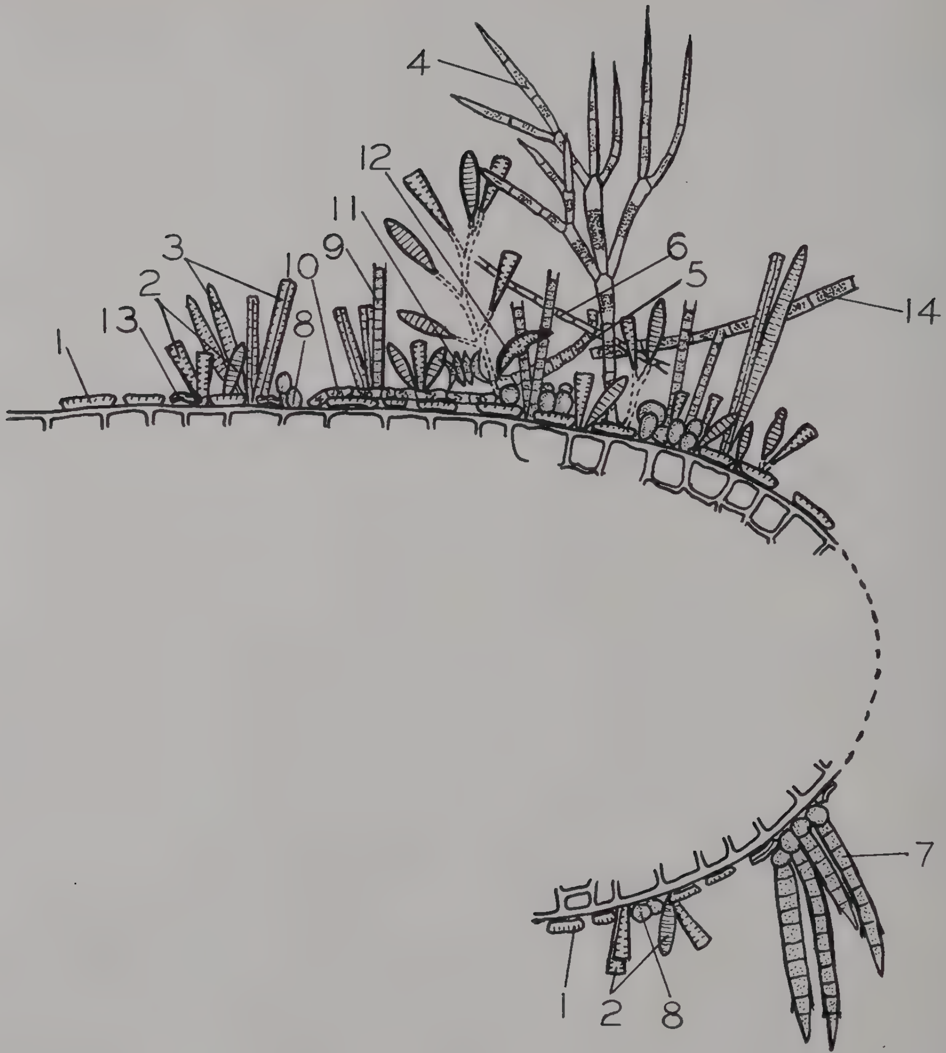

Fig. 1. Sketch of the *Cocconeis-Stigeoclonium* community (aufwuchs) of the hard, fresh-water springs. The algae growing on the upper and lower surfaces of *Sagittaria* leaves are shown in typical position and abundance. From left to right succession from young to older leaves is illustrated. 1. *Cocconeis*, 2. *Gomphonema*, 3. *Synedra*, 4. *Stigeoclonium*, 5. *Fragilaria*, 6. *Melosira*, 7. *Amphithrix*, 8. *Xenococcus*, 9. *Lyngbya*, 10. *Pseudoulvella*, 11. *Scenedesmus*, 12. *Cymbella*, 13. *Achnanthes*, 14. *Microspora*. Sketched from a leaf in Silver Springs, Florida, August, 1953.

atoms not found elsewhere are abundant. These are small species of *Navicula* and *Pinnularia*. Also common on sand are *Cocconeis, Achnanthes, Synedra, Scenedesmus, Merismopedia*, and *Spirulina*.

On wood, the pioneer is *Synedra* followed by *Stigeoclonium, Cladophora*, and *Rhizoclonium*, with *Oedogonium, Lyngbya* and *Chroococcus* common. Painted wood has few species. Certain encrusting blue-greens such as *Schizothrix* form a tough gelatinous layer in which the diatom, *Rhopalodia*, is sometimes abundant and to which *Oedogonium* and *Spirogyra* attach.

Iron surfaces seem to favor green algae such as *Rhizoclonium* and *Stigeoclonium*, although *Phormidium* and *Synedra* attach directly to it also.

A copper screen submerged for several months in Silver Springs pool had a surprisingly large number of algae on it. All were green algae. The filamentous species, *Microspora stagnorum*, formed a mat in which *Sphaerocystis shroeteri*, *Scenedesmus obliquus*, *S. bijuga*, and *S. dimorphus* were abundant. Apparently even in running water, copper inhibits the attactment and growth of most species.

Collections from 12 hard, fresh-water springs have been studied. In addition to Silver Springs, two other large springs have been studied fairly intensively. These are Wakulla and Weekiwachee Springs. Two medium-sized springs from which several sets of collections have been studied are Fanning and Poe Springs. In spite of considerable variation in water quality, the dominant algae and the species of algae are remarkably similar. There is as yet no explanation for certain observations. The presence in considerable abundance of the green alga, *Hydrodictyon reticulatum*, in a few springs such as Weekiwachee and Crystal River; and, the great abundance of *Cladophora* in Wakulla Run in June and its subsequent great reduction in July cannot be explained.

II. The Oligohaline Spring

The oligohaline type of spring is represented by Homosassa Springs (chlorides 570 ppm), Silver Glen Springs (610 ppm) and the "salt boil" at Chassahowitzka Springs. These are large to average in size (flow 190,000 to 265,000 cubic meters per day) with average temperatures (23° to 24°C). They have the typical crater-like boils and broad pools with runs several miles in length. One set of collections only from Silver Glen and Chassahowitzka, have been examined but collections at all seasons from Homosassa for a period of two years have been studied.

Aquatic plants are as abundant here as in the fresh-water springs. Probably *Vallisneria* and *Potamogeton* are more abundant than *Sagittaria* but *Najas* and *Sagittaria* are present in fair abundance.

The chief difference in the algal flora from that of the typical hard, fresh-water spring is the presence, in great abundance, of a coarse species of *Cladophora* not found in fresh-water, along with *Enteromorpha plumosa* in addition to the 5 or 6 dominants typical of the fresh-water type. The diatom, *Cyclotella meneghiniana*, is also abundant in algal mats. Several brackish-water species also are common, such as *Biddulphia laevis*, *Nitschia paradoxa*, and *Stephanodiscus barkleyi*. *Cladophora* and *Enteromorpha* should be placed among the dominants. The flora, therefore, is not characterized by a decided change in species of dominants nor a dropping out of species characteristic of the fresh-water spring. Such fresh-water genera as *Fraglaria*, *Melosira*, *Oedogonium*, *Spirogyra*, and *Mougeotia* are common and relatively about as abundant as in the fresh-water habitats. The change is in the appearance, in great abundance, of the course *Cladophora*, of *Enteromorpha*, and several brackish-water diatoms. These become more abundant as one moves down (toward the Gulf at Homosassa and Chassahowitzka). A few blue-greens which tolerate salt become more abundant. These are *Lyngbya estuari* and species of *Chroococcus*. It is surprising to find, near the Gulf, typically fresh-water genera such as *Spirogyra*, *Oedogonium*, and *Mougeotia* abundant, and in healthy condition, along with typically marine genera such as *Enteromorpha*, *Batotophera*, and *Polysiphonia*.

Aparently when the species *Cladophora graminea*, *Enteromorpha plumosa*, and *Cyclotella meneghiniana* are common and abundant along with the usual freshwater dominants, they indicate an oligohaline condition.

III. The Mesohaline Spring

A single mesohaline spring, unaffected by other conditions, was studied. This is Salt Springs (chlorides 2,800 ppm). Water flows from 9 vertical holes and fissures into a shallow pool at the rate of 195,000 cu m per day. The temperature is 24°C. The broad pool averages about 1.2 m in depth. The run, which is wide and shallow, flows about 6 km to Lake George.

Aquatic plants, especially *Potamogeton pectinatus*, are abundant in open boils, pool and run.

Most fresh-water green and blue-green algae characteristic of the fresh-water spring are absent here. Only one diatom abundant in fresh-water (*Cocconeis placentula*) is abundant. *Potamogeton* and *Enteromorpha* are abundant in pool, run, and in the large boils to a depth of 3 or 3.5 m. In addition to *Enteromorpha*, which forms large tufts on rocks and floating mats in shallow water, *Cocconeis placentula* is very abundant on leaves and plant surfaces. *Lyngbya martensiana*, and *Licmophora flabellata* are also dominant here. Also fairly abundant are *Nitschia paradoxa*, *Mebosira borreri*, and *Cyclotella meneghiniana*. *Amphora coffaeformis* and *Biddulphia laevis* are common along with a second fresh-water dominant *Gomphonema sphaerophorum*. Small tufts of what is apparently a species of *Stigeoclonium* are occasionally encountered. *Surirella striatula* and *Epithemia musculus*, which are not found in fresh-water habitats are rare.

On aquatics in the run 300 m down, in addition to the above species, *Achnanthes lanceolata* is abundant, and *Fragilaria construens* is rare. Thus, the typically fresh-water species have been almost replaced by brackish-water types.

IV. The Sulfide Spring

Collections from 4 springs high in sulfates and hydrogen sulfide have been examined. One of these (Warm Salt Spring) is also high in chlorides, a small one (Hampton) has been so disturbed by man that the algal flora is small, and the third is oligohaline. The fourth (Beacher) is chosen as the one in which the presence of sulfur compounds seems to be the single habitat factor differing from the typical hard, fresh-water type. No complete analysis of the water is available but there is good evidence that it is a typical hard, fresh-water type with high sulfate and hydrogen sulfide, but devoid of oxygen. (Data on water conditions in Beecher Spring are in press, Odum and Caldwell, Copeia.)

The flow, which is estimated at about 6,000 cu m per day, is from three principal fissures. Two flow into a shallow, shady head-pool and one is on a short side run. The pool is small and shallow (1.2 m) and has a soft bottom of malodorous organic ooze 0.6 m deep. Logs, stems, and leaves are abundant. There are no aquatic flowering plants but mosses are common and white sulfur bacteria clothe all stone and wood surfaces.

The run is shallow, narrow and shady and unlike most others in that it consists of alternating riffles and pools and the bottom has some 20 cm of the same organic ooze as does the pool. About one kilometer down, it has been partially dammed and broadens into an open sunny pool about 15 m wide, and 1.2 m deep, with a sandy bottom. In this pool and somewhat above it, *Vallisneria* is abundant. In the pool, the spatterdock (*Nuphar*) grows, along with an abundance of emergent aquatics such as *Saururus* and *Typha*. Below the pool, the run again becomes shallow and rapid. Part of the water from the lower run is diverted into state fish-hatchery ponds.

In the pool, the dominant, and abundant, algae are blue-greens, especially *Lyngbya*, *Phormidium* spp., and *Spirulina subsalsa*. *Aphanocapsa*, *Spirulina gomontii*, *Chroococcus turgidus*, and *Gleocapsa gigas* are also present. At the surface, a small species of *Navicula* and one of *Synedra* are sparse and the only diatoms present.

About 25 m down, the run, after flowing over several riffles, broadens into a shallow pool. The bottom is covered with large gelatinous globules of a species of *Aphanothece*. On the bottom and especially in the shallows, a medium-sized species of *Spirogyra* is very abundant, along with the blue-green algae found in the pool and boil.

About 200 m down the run, a species of *Cladophora* becomes abundant and the *Spirogyra* less so. On *Cladophora*, *Gomphonema longiceps* and *Eunotia pectinalis* are abundant. *Oscillatoria princeps* is abundant on the bottom. On the surface, *Phormidium autumnale* forms mats in which a species of *Anabaena* and of *Closterium* are common.

In the large pool, especially at the surface and on leaves, the typical fresh-water springs algae become abundant along with a few additional species. On the bottom, blue-greens still are most abundant. Below the pool, the flora seems almost identical to that of the typical hard, fresh-water run.

All the other sulfur springs, whether fresh, oligohaline, or mesohaline, have also a dominant flora of blue-green algae. The absence of dissolved oxygen and the presence of hydrogen sulfide, which is probably produced by the reduction of sulfates by sulfur bacteria, seem to be the important habitat factors. The abundant blue-green algae are probably species which use hydrogen sulfide as a hydrogen source in photosynthesis.

If not saline, the water from the sulfur springs develops a flora quite similar to that of the typical hard, fresh-water type as soon as it becomes aerated and loses most of its hydrogen sulfide.

The Algal Flora of Warm Salt Spring

A spring which differs in several ways from all others studied is Warm Salt Spring. It is the most saline (chlorides 9,350 ppm) of any known Florida spring, it is about 9° C warmer than any (30°C), and is devoid of oxygen and very high in sulfates (1,700 ppm) and hydrogen sulfide. A single, large and very deep vertical vent discharges into a broad circular pool at the rate of about 25,000 cu m per day, and this in turn into a narrow shallow run which flows about 6 miles to the Gulf.

There are no aquatic flowering plants in either pool or run but there are sparse beds of *Chara honemani* in the shallows of the pool. The bottom of the pool which is about 2 m deep at the boil rim, is covered with a thin layer of organic ooze. The run is of alternating riffles and shallow pools.

The algal flora consists largely of filamentous and colonial blue-green algae with a single abundant species of diatom (*Nitschia gandersheimensis*). In the run, a coarse species of *Cladophora* is abundant and a large species of *Vaucheria* forms extensive mats at the edge. On and among these, 5 or 6 species of diatoms are abundant. These are apparently brackish-water or marine species.

Not a single important species found here has been collected in any other spring.

DISCUSSION

As pointed out above, and as shown in the table (Table I), the dominant species of algae in the boil, pool, and run are the same in the hard fresh-water type spring. This is true also of the oligohaline type. The only exception is at the pool edge where there is little current.

In the mesohaline spring, there seems to be some difference in the species in boil and pool as compared with the run. This is definitely true of the sulfide spring, Lack of dissolved oxygen is almost certainly the important factor here. Increased aeration down run brings about a change in dominant species.

The classification of the springs into six types as to water quality seems valid since there is a reflection of this classification in the algal floras of four and possibly five of these types. No correlation between chemical composition and algal floras could be found except these. This is true in spite of the fact that there is considerable variation in mineral salts content among the springs. While calicum and phosphorus are high in the hard, fresh-water springs there is great variation in other important minerals such as nitrate. The nitrate content is low but there is a variation of about 400 per cent among the springs studied (0.5 to 2.0 ppm), with no apparent effect on the type of flora. Variation in the carbon dioxide and oxygen content likewise seem to have little effect on the flora unless oxygen is completely absent.

These observations seem to point to the importance of current. If one agrees with Ruttner and other workers that a film of water impoverished in mineral salts forms around organisms in quiet water, and that this film is swept away by a current which constantly renews these vital elements at the cell surface, exchange between an organism and its environment will be rapid even where the actual diffusion gradient is low. The writer believes this is a very important factor in streams. Observations both here and in streams in North Carolina, as well as inferences drawn from other papers on plant and animal life in streams, seem to bear this out. This current effect has been neglected by most ecologists and limnologists. The exact speed of current necessary to sweep away the surface film and bring about this rapid exchange is unknown, but observations indicate the minimum is about 15 cm per second.

Although current is very constant and uniform at any one point in a spring, it varies considerably in different places in a large boil, pool, and run. Next to light it is the most important variable habitat factor. On the other hand, current brings about the great uniformity of temperature in spring and run. Furthermore, by causing constant oscillation of leaves and stems, it increases light penetration into beds of plants.

The major algal communities of four of the types of springs are all lotic *aufwuchs* biocoenoses. If one designates these by dominant genera they are:

1. The *Cocconeis-Stigeoclonium* community of the hard, fresh-water springs, in which the important habitat factors are a constant supply of hard, fresh-water at constant temperature and flow, with some seasonal variation in light intensity and duration.
2. The *Cladophora - Cocconeis - Enteromorpha* community of oligohaline springs, in which conditions are the same as in the hard, fresh-water spring except that sodium, potassium, and chlorides are high (chlorides 100 to 1,000 ppm).
3. The *Enteromorpha - Lyngbya - Licmophora* community of mehohaline springs in which conditions are the same as in the hard, fresh-water springs except for greater salinity (chlorides 1,000 to 10,000 ppm).
4. The *Phormidium-Lyngbya* community of sulfide springs, in which the important habitat factors are a current of constant-temperature water, devoid of dissolved oxygen, and high in sulfates and hydrogen sulfide.

As pointed out above *Chara* and *Vaucheria,* and possibly *Plectonema,* should be regarded as part of the community of higher plants of the rapids in which *Najas* and *Sagittaria* are the dominants.

SUMMARY

Evidence is presented that there are the following types of Florida springs, as indicated by water quality and algal flora: hard, fresh-water; oligohaline; mesohaline; and sulfide. There are probably two other types: soft, fresh-water; and mesohaline-sulfide.

There is one important algal community in each type of spring and its run, or stream—a lotic *aufwuchs* (or periphyton) community in which diatoms are usually dominant.

The importance of current in constantly renewing minerals and gases at the plant surfaces is emphasized.

The following algal communities are recognized:

1. The *Cocconeis-Stigeoclonium* community of hard, fresh-water springs.
2. The *Cladophora - Cocconeis - Enteromorpha* community of oligohaline springs.
3. The *Enteromorpha - Lyngbya - Licmophora* community of mesohaline springs.

4. The *Phormidium-Lyngbya* community of sulfide springs.

The species of algae attaching to various types of substrata are given as well as succession on young to older leaves.

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NATURAL RESTOCKING OF FORESTS FOLLOWING THE 1938 HURRICANE IN CENTRAL NEW ENGLAND[1]

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The New England hurricane of 1938, by destroying many acres of mature and semi-mature forests, initiated new forest associations over a large area. During a decade at the Harvard Forest at Petersham in central Massachusetts, the author was able to participate in a number of studies on the development of these new associations under a variety of conditions. These primarily involve successions following the blowdown of old-field white pine on glacial till soils, although other conditions are also represented.

The available data consists of a series of 14 permanent sample plots, mostly $\frac{1}{10}$ acre in size, established in 1940 on various blowdown sites in the Harvard Forest; and a large number of temporary sample plots in the Forest and surrounding townships. These data provide an insight into the development of secondary forest successions following blowdown in central New England with reference to: (1) the relationship of soil types to post-hurricane regeneration, (2) the effect of previous forest association upon the restocking, and (3) the importance of other factors, particularly whether or not the down timber was subsequently logged.

DAMAGE AND SALVAGE

The New England hurricane of September 21, 1938, was one of the most destructive storms in the history of the United States. Considering the damage to the forests alone, nearly 3 billion feet of timber were blown down on more than 600,000 acres of forest land. Damage was severe throughout New England except in Maine and a narrow strip along the New York state line. In the white pine-hardwood region alone, nearly one-half by volume of the total softwood timber stand was destroyed (Baldwin, 1942).

In the Harvard Forest, at least two-thirds of the merchantable sawtimber was uprooted or left as broken snags. According to Rowlands (1939), more than half the timber was blown down on 43 per cent of the area of the Harvard Forest. Of the stands more than 40 years old, 93 per cent of the softwoods were blown down, together with 57 per cent of the mixed-wood stands and 38 per cent of the hardwood stands. On the other hand, few of the younger stands of timber were seriously damaged.

Throughout the region, salvage operations were started immediately following the storm. The New England Timber Salvage Administration was established by the U. S. Government to promote logging and to purchase logs. By the end of 1942, this agency had handled about 700 million board feet. During the same period, some 90 million feet were salvaged on the White Mountain National Forest and nearly 600 million feet were cut by private agencies throughout the region (Baldwin 1942). The war accelerated salvage operations somewhat, but also caused many mill opperators to seek stands more profitable to operate, thus resulting in ever greater forest depletion.

In addition to the salvage operation, considerabe clean-up work was done, principally to reduce the fire hazard. The New England forest emergency project supervised slash disposal, fire lane construction, and other hazard production work on over 200,000 acres, while private owners cleaned up more than 100,000 additional acres.

Relatively little research has been carried out on the effects of the hurricane on the forests. Curtis (1943) published some observations on susceptibility to wind damage . Bess (1944) investigated insect damage following the storm and concluded that practically no standing trees were killed by bark beetles. Cline (1939)and the Committee on Silviculture of the New England section, Society of American Foresters (1941) recommended that reliance be placed on natural reproduction for the restocking of blowdown areas, but the recommendation was made in advance of the appearance of the results of natural restocking surveys.

PREVIOUS RESTOCKING SURVEYS

A small number of surveys have been carried out to obtain information on the rehabilitation of hurricane-damaged forest areas by natural restocking.

Cheston (1940) studied natural regeneration on the Keene (New Hampshire) and Union (Connecticut) forests of the Yale School of Forestry one year after the hurricane. He found that from 24 to 32 per cent of the heavily damaged areas studied were covered by slash, a smaller percentage of the area being unstocked, and the remainder restocked about equally with desirable and inferior species.

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[1] Based upon data collected while the author was a member of the staff at the Harvard Forest, 1944-50. The paper is derived from a portion of a doctoral dissertation submitted to Yale University.

Natural regeneration on white pine lands in the Fox Research Forest at Hillsboro, New Hampshire, was studied by Baldwin (1940), two years after the hurricane. Although he found an average of 16,000 stems per acre on blowdown areas, only one-half consisted of valuable species; and these were highly irregular in their distribution, areas up to one-half acre in size being virtually devoid of valuable stems. Baldwin's 61 mil-acre plots were divided between three soil types, and differences in composition between these soil types were apparent. White pine was found to be much more abundant on the sandy Danby soil than on the heavier Herman and Canaan soils. Red oak, sugar maple, and gray birch, all important on the heavier till soils, were completely lacking on the Danby soil. Paper birch was apparently more abundant on the shallow Canaan soil than on the deep but otherwise similar Hermon type.

In 1941, after two growing seasons had passed since the hurricane, Brake and Post studied the restocking on 137 former old-field white pine areas in north-central Massachusetts. They concluded that, on the better sites, sufficient volunteer reproduction of the better elements was present in most cases to make possible the development of well-stocked timber stands of good quality. On the poorer sites, reproduction was much less adequate. They found that 98 per cent of the better sites had more than 500 desirable stems per acre, while 88 per cent had more than 1000 stems. On the average sites, 93 per cent had more than 500 stems, and 77 per cent more than 1000 stems. On the poorest sites, however, 84 per cent had more than 500 stems, while only 42 per cent had more than 1000 stems per acre.

An intensive study of the natural restocking on one compartment (Tom Swamp III) of the Harvard Forest was understaken by Larson, Yoder, Gill, and Praher in 1942 under the direction of R. J. Lutz and the writer. Twenty-three stands were included in the study, representing four principal soil types and several former cover types. Adequate restocking was found on all but the wettest areas.

SURVEY METHODS

In the various restocking surveys carried on at the Harvard Forest, methods of surveying the vegetation were modified from time to time.

Permanent sample plots $\frac{1}{10}$ to $\frac{1}{46}$ acre in size were established to follow changes in volunteer stands over a period of years. Although these give a clearly inadequate measure of restocking over a given stand since only one plot was established per stand, they do provide important information on changes from year to year.

In the evaluation of current restocking, reliance was placed upon mil-acre plots or quadrats, 6.6 feet square. In the earlier surveys, these plots were located systematically (*i.e.,* mechanically) in a regular grid, 20 to 50 on each area depending upon its size. Later, a continuous strip of 50 mil-acre plots was run, starting at a point chosen at random, and running at right angles to main topographic features (*i.e.,* up or down the slope). While this single strip technique did not cover the area as well as mechanically-spaced plots, and consequently gave a less accurate picture of a particular area, it did save a great deal of time, and permitted the study of many more tracts.

MEASUREMENT OF STOCKING

The amount and adequacy of natural reproduction can be measured either in terms of abundance (stems per acre), or frequency (per cent of quadrats stocked). In the earlier studies, the numbers of stems per acre was determined for each species and for each type of origin (seedlings, stump sprouts, seedling sprouts, or root suckers). These abundance values give a good record of stand condition, but have two drawbacks. First, every stem on the mil-acre plots must be counted and tallied, often a very arduous task. Then, despite the great amount of work involved, no measure is obtained of the distribution of the reproduction over the area. Abundance values may be quite accurate and yet give no information as to whether the stems are distributed throughout the stand or densely concentrated in a small area.

To overcome these difficulties, frequency rather than abundance has been increasingly used in restocking surveys (Lowdermilk 1927, Haig 1929, 1931). The term *frequency* (also *frequency index* or *frequency per cent*) refers to the number of quadrats that are stocked with a given species or group of species. The unit of restocking, then, is the quadrat rather than the tree, and frequency value will be affected by the size of the quadrat adopted. The mil-acre quadrat was used in most of the present studies because it is conventional, convenient to handle in the field, and simple to compute. Furthermore, a spacing of 6.6 feet approximates that of the normal forest plantation. A stand restocked with a frequency of 100 will have at least 1000 well-spaced stems per acre and would be considered full-stocked by most standards.

In order to compare the results obtained by the two measures of stocking, 540 mil-acre plots were tallied in a total of 20 stands in one compartment (Tom Swamp III) in such a way that the data could be worked up in terms of both frequency and abundance. The two measures yielded similar results although certain differences were apparent. For instance, there were more than twice as many yellow birch seedlings as white ash in the area (abundance), but the ash are more widely distributed (frequency). An examination of the data indicates that the yellow birch seedlings are concentrated in the lower and moister sites.

Similarly, comparisons are afforded by Tables I and II summarizing a study where frequency is based upon the percentage of stands in which the species occurs; and by Tables III and IV summaring a study where frequency is based upon the standard mil-acre plot. In each case, the two measures yielded results comparable in general but differing in detail. In each case, more information could be gleaned from the two analyses than from one alone.

TABLE I. 1941 natural reproduction study soil types and seedling abundance in seedlings per acre

Species	Charlton	Gloucester	Merrimac	Hinckley	All
Gray birch	1830	2200	720	620	1820
Pin cherry	2840	520	740	600	940
Black cherry	800	720	790	400	710
White pine	660	640	1060	850	710
Red maple	510	720	620	230	620
Red oak	250	150	80	60	160
Paper birch	330	60	20	10	90
White ash	40	120	20	20	90
Aspen	100	80	110	20	80
Black brich	40	50	20	10	40
Sugar maple	10	40	..	20	30
Hemlock	130	10	..	10	30
White oak	10	20	20	10	20
Balsam fir	10	10	..	..	10
Yellow birch	40	10	..	..	10
Hickory	10	10	10	..	10
Red spruce	20	10	..	..	10
Beech	10	10	..	..	10
Basswood	10	10	..	..	10
Scrub oak	..	..	20	..	10
All Species	7650	5390	4230	2860	5410
Number of stands	22	82	12	15	131

SOIL TYPES AND RESTOCKING

The young forest stands dating from the 1938 hurricane provide an opportunity to examine the relationship existing between soil types and forest composition. In two studies, variables other than soil type were kept as uniform as possible in field sampling. All of the timber was, of course, destroyed on September 12, 1938, and the ensuing stands were of a single age. The previous cover in all cases was predominantly white pine. Finally, the sampling was undertaken two or three growing seasons after the blowdown so as to provide sufficient time for the new growth to become established, and yet not enough time for competition to greatly reduce the number of seedlings.

The first study consisted of 3,400 mil-acre plots taken in 137 former white pine stands in northern Worcester County by Brake and Post in 1941 and used by them as the basis for their master's theses.

TABLE II. 1941 natural reproduction study soil types and seedling frequency as per cent of stands in which the species occurs

Species	Charlton	Gloucester	Merrimac	Hinckley	All
Red maple	100	99	67	87	95
Pin cherry	100	88	83	87	89
Black cherry	86	93	75	87	89
White pine	86	89	83	100	89
Gray birch	100	82	67	73	82
Red oak	77	77	25	40	68
Aspen	27	38	33	20	34
Paper birch	50	31	17	7	30
White ash	32	23	17	13	23
Sugar maple	14	21	..	7	16
Black birch	14	20	8	7	16
White oak	9	17	17	13	15
Hemlock	27	7	..	13	11
Hickory	5	10	8	..	8
Yellow birch	23	5	..	..	7
Balsam fir	5	5	..	..	4
Beech	5	5	..	..	4
Red spruce	5	1	..	..	2
Basswood	2	1	..	..	2
Scrub oak	..	..	8	..	1
Number of stands	22	82	12	15	131

TABLE III. Seedling abundance in Tom Swamp III, 1942

Species	Gloucester stony phase	Gloucester	Charlton	Sutton	Whitman	All
Red maple	908	2139	1668	558	519	1392
Yellow birch	204	671	508	1692	1046	753
White pine	1029	1030	643	525	106	679
Black cherry	158	994	822	616	125	647
Red oak	662	250	778	616	236	483
Pin cherry	150	1168	116	158	19	420
Gray birch	1054	675	92	300	125	390
White ash	558	539	236	176	206	346
Black birch	404	369	411	100	92	303
Paper birch	129	204	77	41	86	118
Sugar maple	46	16	114	25	25	51
White oak	..	46	39	33	..	29
Hemlock	..	..	72	25	8	26
Aspen	16	41	17	..	..	19
Hickory	46	25	..	..	..	12
Basswood	..	..	..	..	38	8
Total	5364	8167	5593	4865	2631	5676

The second consisted of 600 mil-acre plots in a small area taken by Larson, *et al.* from a single compartment in the Harvard Forest. In each case, the original field notes were reanalyzed by the present worker to determine what differences in forest composition could be attributed to soils type. The results were compiled for seedlings only, leaving out seedling sprouts, stump sprouts, and root suckers, all of which owe their presence to the preceding stand. Results were compiled on both abundancy and frequency bases.

TABLE IV. Seedling frequency in Tom Swamp III, 1942

Species	Gloucester stony phase	Gloucester	Charlton	Sutton	Whitman	All
Red maple	49	53	52	29	20	43
Black cherry	14	38	40	26	14	30
Red oak	46	20	41	24	19	29
White pine	41	32	32	24	8	27
White ash	44	27	16	11	16	19
Yellow birch	9	17	18	25	18	18
Pin cherry	8	32	11	12	2	15
Black birch	28	16	14	9	8	14
Gray birch	14	23	3	24	8	13
Paper birch	6	11	6	4	3	7
Sugar maple	4	2	9	2	3	5
White oak	..	6	3	..	..	3
Hemlock	..	..	6	5	1	2
Aspen	2	4	..	..	..	2
Hickory	8	2	..	..	..	1
Basswood	..	..	..	..	2	1

Of the stands sampled by Brake and Post, 131 were found to be on Charlton, Gloucester, Merrimac, or Hinckley soils on the basis of the soils map published by Latimer, *et al.* (1927). All are well-drained upland soils. Charlton and Gloucester soils are derived from late Wisconsin glacial till, the Charlton parent material being predominantly Brimfield Schist while the Gloucester parent material is predominantly granite. Merrimac and Hinckley soils are derived from glacial outwash, Merrimac occurring in sand plains laid down by aggrading glacial meltwater streams, while Hinckley occurs in kame deposits formed by meltwater coming directly off the ice. Theoretically, the till soils, being loams, should support a richer flora than the outwash soils which are sands. Of the tills, the Charlton is derived from the richer and more easily decomposed parent material and should be the more fertile. Of the outwash sands, Merrimac has the higher water table and should provide the better site.

Tables I and II give the abundance and frequency respectively of seedlings of various species on these soil types. That the till soils were better stocked than the outwash soils, and contained a better representation of the mesophytic species can readily be seen. There is little significant difference in stocking between the Charlton and Gloucester soils, however. The Charlton soil had more seedlings per acre, but the difference is entirely attributable to the great number of pin cherry seedlings. On the frequency basis, the restocking was comparable. Likewise, there is little if any significant difference in composition of restocking between the Merrimac and Hinckley soils. Although several species are more abundant on the Merrimac soils, the same species are more frequent on the Hinckley soils.

Of the light-seeded pioneer species, gray birch (*Betula populifolia* Marsh.), pin cherry (*Prunus pensylvanica* L.), and black cherry (*P. serotina* Ehrh.) had seeded in profusely on all sites, but with somewhat better success on the till soils. Paper birch (*B. papyrifera* Marsh.) and aspen (*Populus tremuloides* Michx. and *P. grandidentata* Michx.), being south of their optimum range, were less well represented. None of these species, however, could be expected to maintain dominance in the stand after forty or so years in central New England.

Three longer-lived species, white pine (*Pinus strobus* L.), red maple (*Acer rubrum* L.), and red oak (*Quercus rubra* L. and including in these studies, black oak, *Q. velutina* Lam.), had also become established in substantial numbers. White pine was more abundant upon the outwash sands where it is the characteristic species in older stands, while red maple and red oak were more common on the till soils where they are the characteristic species in older stands (Spurr 1950). These three would seem to be the dominant species in the new stands.

On the till soils, a number of mesophytes were found. These included white ash (*Fraxinus americana* L.), black birch (*B. lenta* L.), yellow birch (*B. lutea* Michx.), sugar maple (*A. saccharum* Marsh.), hemlock (*Tsuga canadensis* (L.) Carr.), and occasional beech (*Fagus grandifolia* Ehrh.), balsam fir (*Abies balsmea* (L.) Mill.), red spruce (*Picea rubens* Sarg.), and basswood (*Tilia americana* L.). There is some evidence that the yellow birch and hemlock were more successful on the Charlton soils than on the Gloucester. Some of these trees also occur infrequently on the outwash sands.

Finally, three xerophytes were found scattered on the outwash and occasionally on the tills. These include white oak (*Q. alba* L.), scrub oak (*Q. ilicifolia* Wang.), and hickory (*Carya* spp.).

The 1942 study of Tom Swamp III gives much information about a small tract. All the blowdown areas in a small compartment were heavily sampled. Five soil types were included: Gloucester stony fine sandy loam, shallow phases, on the top of a low ridge; Gloucester stony fine sandy loam, a little lower on the ridge; Charlton stony fine sandy loam; Sutton stony silt loam; and Whitman stony silt loam. Sutton is the imperfectly drained and Whitman is the poorly drained member of both the Gloucester and Charlton soil catenas. The Charlton soils occupy somewhat lower and moister sites than the Gloucester soils so that differences in composition attributable to these two series may be as much due to moisture differences as to fertility differences.

Natural restocking after the hurricane by seedlings of all species did not differ appreciably between the three upland soils (Tables III and IV), but total restocking was somewhat poorer on the imperfectly drained Sutton soil, and markedly poorer on the poorly-drained Whitman soil.

Very little difference is apparent for the individual species between the restocking on the three upland soils. Perhaps the most obvious correlations between composition and soil are provided by white pine and yellow birch. The former is most common on the driest soils and decreases with increasing soil moisture, while the latter is most common on the Sutton soil and decreases with decreasing soil moisture. White ash is actually both more frequent and abundant on the Gloucester soil than on the Charlton, thus seeming to indicate that it has little preference for the supposedly richer Charlton. Several of the light-seeded species, especially the birches, had apparently become established in greater numbers on the drier soils. Eliminating these, an eventual red oak-red maple-white pine-white ash association could be predicated with yellow birch, black birch, and perhaps including paper birch as being locally abundant.

The first study clearly demonstrates that the till soils (Charlton and Gloucester) support a richer tree flora than the outwash soils (Merrimac and Hinckley). The second study suggests that the restocking is most successful on the well-drained tills (Gloucester and Charlton) rather than on the excessively drained Gloucester stony phase, or the more poorly drained Sutton and Whitman soils. In neither study, however, is there any clear evidence of differences between two soil types of the same drainage and same particle size (*i.e.*, between Gloucester and Charlton, or between Merrimac and Hinckley). We may conclude, therefore, that the differences in restocking are largely attributable to differences is soil texture and moisture, and not to parent material differences where texture nad moisture are the same.

Previous Stand and Restocking

The 14 permanent sample plots in the Harvard Forest provide an opportunity to study the changes in restocking with time on various combinations of previous stand and soil type. Eight of the plots were located on glacial till and 6 on outwash. Of the till plots, 6 followed old field white pine, one followed an immature white pine plantation on an old field, and one followed hardwoods. Of the outwash plots, one followed selectively cut white pine and 5 followed old-growth white pine and hemlock.

The changes in abundance from 1940 to 1948 are presented for the 6 plots following old-field white pine on glacial till in Table V. All are on well-drained sites. Although short-lived species such as black cherry (largely eradicated in early years by tent caterpillar defoliation and suppression), pin cherry, gray birch, and aspen make up ⅓ of the 1948 stand, considerable numbers of longer-lived species also occur. Perhaps the most notable feature is that, except for the seedling white pine, paper birch, and gray birch which largely became established in 1941, there has been little change in the restocking since the plots were established. In other words, the restocking 10 years after the hurricane is very largely made up

Table V. Natural restocking on permanent sample plots. Six plots following old-field white pine on glacial till

Species	Abundance (stems per acre)				
	1940	1941	1942	1944	1948
Long-lived trees					
Red maple	1470	2000	1590	2160	1280
White ash	790	890	770	980	890
White pine	...	260	240	470	390
Red & black oak	320	520	400	370	320
Paper birch	...	290	260	220	200
Black & yellow birch	130	40	120	160	200
White oak	70	60	110	80	90
Sugar maple	30	10	10	10	20
Others (Hem., Hick., Basswd.)	..	..	10	10	10
Total	2810	4070	3510	4460	3400
Short-lived trees					
Black cherry	3300	2500	1100	1800	980
Gray birch	100	590	400	320	490
Aspen	250	290	190	270	240
Total	3650	3380	1690	2390	1710
Total	6460	7450	5200	6850	5110

Plots A (P.H.IV.), F (T.S.V.), G (T.S.VI.), H (T.S.I.), I (T.S.I.), J (S.C.II).

of the plants present in the understory at the time of the hurricane plus pioneer species that became established shortly after the hurricane.

Of the long-lived species present today, there is every reason to believe that red maple and red oak will continue to make up the dominant stand. The white pine is largely suppressed by the hardwood growth and may be expected to largely disappear. The white ash, paper birch, black birch, and yellow birch cannot compete overly well with the aggressive oak and maple and should become less important as the years go by. In other words, the post-hurricane stands followed old field pine will evolve into a red oak and red maple association with lesser quantities of white ash and the birches; this is the same association that is known to follow the clearcutting of old field pine and that is described as the transitional type on well-drained soils.

Confirmatory information on a frequency basis is provided by data from 6 small blowdown areas in the southeast corner of the Tom Swamp Block, considered by some as representing the best sites in the forest (Table VI). Again it may be seen that a red oak-red maple association is the result of the blowdown of old field white pine on well-drained glacial till. In this case, white ash and black birch will apparently be the chief secondary species since the gray birch is short-lived and the black cherry and white pine cannot be expected to survive in any number.

In contrast to the above cases, where the hardwood advance growth under the previous pine stand accounts in large measure for the post-hurricane stand, are cases where immature pine stands were blown down at a time when their density was still great enough to prevent the establishment of an understory. The example of plot B (P. H. I.), a 28-year-old dense white pine plantation in 1938, is typical. In 1940, there were 9840 pin cherry seedlings per acre and only 120 others of which 80 were red maple and 40 red oak. Eight years later, the only changes were a slight increase in the pioneer species marked by the addition of 520 white pine seedlings, 280 gray birch seedlings, and 160 additional red maple seedlings. With no advance growth from the previous stand, the restocking is inadequate even after 10 years. This is true not only for the case cited, but for all similar instances of the blowdown of dense pine plantations and other stands where no advance growth was present.

TABLE VI. Frequency of restocking under favorable conditions Tom Swamp I. and II., 1942

Species	Seedlings	Seedling sprouts	Stump sprouts	All elements
Red oak	31	11	..	41
Red maple	27	13	5	38
White ash	11	13	1	24
Gray birch	21	..	x	21
Black cherry	18	2	..	19
Black birch	12	1	1	14
White pine	12	..	..	12
White oak	6	3	x	8
Yellow birch	5	3	..	7
Sugar maple	3	2	x	6
Paper birch	5	..	..	5
Aspen	3	..	..	3
Basswood	1	1	..	2

Based upon 300 mil-acre plots in 6 small blowdown areas.
x Indicates species present but at frequency less than 0.5 percent.
Species not listed but occurring at low frequency include beech, hickory, black oak, hemlock, red spruce, and large-toothed aspen.

Hardwood stands were generally more resistant to hurricane damage than softwood or mixed-wood stands, and only one permanent plot was established in hardwood blowdowns (Plot D, T.S. IV). Total restocking increased slowly from 3000 stems per acre in 1940 to 4460 in 1948. Red maple (580), white pine (760) and the birches (1940) were the most abundant species in 1948. Again, however, the pine was largely suppressed

TABLE VII. Natural restocking on permanent sample plots. Five plots following old growth white pine and hemlock on glacial stratified drift

Species	ABUNDANCE (stems per acre)				
	1940	1941	1942	1944	1948
Long-lived species					
White pine	580	670	650	860	570
Red maple	260	290	160	200	170
Paper birch	..	20	150	20	100
Red oak	70	80	140	170	90
White ash	50	110	60	50	50
Hickory	..	20	40	20	40
White oak	10	20	30	40	30
Hemlock	20	20	..	10	10
Basswood	20	20	10	20	10
Sugar maple	20	10	..	..	10
Black birch	30	..	10	..	x
Yellow birch	..	x	10	10	x
Beech	30	20	10	10	x
Elm	..	x	10	..	x
Total	1090	1280	1280	1410	1080
Short-lived species					
Pin cherry	610	840	860	900	420
Gray birch	40	310	300	340	310
Black cherry	50	120	100	210	90
Aspen	10	90	80	70	40
Total	710	1360	1340	1520	860
Total	1800	2640	2620	2930	1940

x Indicates species is present with frequency less than 5 percent.
Plots C (T.S.IX.), E (T.S.IV.), K (S.C.IV.), L (S.C.IV.), M (T.S.IX.).

even 10 years after the storm. Red oak (100) and hemlock (90), though not as abundant, were represented by large vigorous stems, and the eventual emergence of a hemlock-red oak-red maple association can be postulated.

A better sample is available for hurricane blowdown areas following old-growth white pine and hemlock stands on glacio-fluvial outwash sands (Table VII). Of the 5 plots, one is at the Boulder Site in Tom Swamp IV, two are located in the old Barre Woods along the Swift River in the Slab City Block, and one is located in Tom Swamp IX. On the latter plot, which represents the driest site, little restocking of any kind had become established in 10 years, but the average of the 5 shows a good restocking of white pine together with a scattering of various hardwoods. Obviously, the restocking on the excessively-drained sands is much less adequate than on the glacial tills, a fact previously indicated by the mil-acre temporary plot surveys. Equally important, however, is the apparent fact that the white pine is successfully reestablishing itself on these "natural white pine soils," while the hardwoods are few in number and are not particularly vigorous.

A final case deals with natural reproduction in a selectively cut white pine stand on sandy soil after the residual stand was blown down by the hurricane (Plot N, T.S. IX). Here the composition is similar to that for the uncut old-growth in Table VII, except that the restocking is more abundant. Total restocking increased from 3440 in 1940 to 3980 in 1948, with white pine (1320-1650), red maple (1040-1130), and red oak (560-500) being the most abundant species. Short-lived pioneer species (gray birch, cherries, aspen) were few in number (160-460) compared to the better sites. The year by year tally indicates that the present stand was established prior to the hurricane, that it was released from the understory by the blowdown of the overstory, and that it had changed little in composition from 1938 to 1948.

In general, it would appear that the young stands following the logging of hurricane blowdown stands are generally similar to the hardwood stands that normally follow logging in the same area. On glacial tills, red oak-red maple association seems to be the rule together with such minor components as are characteristic to the soil drainage and the locality. On stratified outwash sands, a white pine-red oak-red maple stand seems to be emerging on most sites.

Effect of Logging and Miscellaneous Factors on Restocking

Both the temporary and the permanent sample plot data indicate the great importance of residual trees and advance growth in forming the new stand. Much of the present stand on blowdown areas is derived from advance growth under the old stand. Where there was no such growth, present restocking is inadequate, and the areas could well have been planted. In other words, it appears that the blowdown areas did not provide sites favorable to the establishment of new growth. Only pioneer species such as pin cherry and gray birch were able to invade these areas in any number. Even white pine could not establish itself in any great number in blowdown sites on sandy soils, and has come in on the glacial till soils only after hardwoods have developed.

Since the new stand is largely evolved from advance growth and residuals, the size of the blowdown and the propinquity of seed supply does not appear to be particularly important in determining the character of the restocking. Actually, most of the blowdown areas are confined to a few acres in size since the pre-existing stands were comparably small and since the hurricane frequently tended to blow down patches of trees rather than everything. Even where large timber occupied large areas, however, and was completely blown down, the character of the new growth does not appear to be different from that in the typical small opening.

All the tracts considered in the above survey were logged after the hurricane. They may therefore be considered as cutover areas as well as blowdown areas, and it is not therefore surprising that the restocking on them is similar to that found on areas of standing timber cutover before and since the hurricane. A restocking survey of the Pisgah tract is thus of considerable interest in that it throws light upon post-hurricane regeneration in the absence of log salvage.

The Pisgah tract is a 20-acre stand of primeval forest in Winchester, New Hampshire, owned by Harvard University. It is one of a number of stands in that locality which have been studied intensively (Cline and Spurr 1942), and was completely blown down in 1938. No logging was done, however, on the argument that the windthrow was a natural disturbance and that the prostrate stand was in every sense as much a virgin forest as the pre-existing old growth white pine and hemlock.

In the summer of 1942, four growing seasons after the hurricane, a transect was run from the top of the ridge dominating the east portion of the tract southwest across the topography to the end of the blowdown timber. Seventy mil-acre plots were tallied by the stocked quadrat method.

Conditions following blowdown on this virgin timber tract differed very greatly from those on second-growth areas. The tangled blowdown of heavy timber (largely hemlock and white pine) was 4 to 10 feet thick over most of the area. Under this criss-cross of logs, the soil was moist and relatively undisturbed except around the uprooted stumps. The boles of the fallen trees covered over 30 per cent of the area, and inasmuch as most of these were suspended several feet from the ground, they affected practically all of the surface. Mineral soil was exposed in stump pits on about 8 per cent of the area. Rock outcrops, either naked or covered by a thin organic layer, were prominent on another 15 per cent of the transect. Wet Whitman soil covered somewhat less than 5 per cent of the area, the remainder being a shallow phase of Hermon (the podzol equivalent of Gloucester).

The tree reproduction differed between high slopes and low slopes (Table VIII). On the high slopes (26 plots), seedlings of paper birch, red maple, black cherry and black birch predominated. Little advance growth of any kind had persisted. The stand on the low slopes (44 plots), however, was dominated by hemlock and beech advance growth. Seedlings of other species were present but most seemed likely to be soon overtopped. Yellow birch occurred instead of the black birch of the high slopes.

The beech recorded was all advance growth except for one seedling. About sixty per cent of the hemlock consisted of advance growth, most of this occurring on low slopes. The advance growth ranged up to 10 and 15 feet in height and much of it had persisted for many years under the old stand. Hemlock seedlings were equally as common on high as on low slopes. The other trees present consisted almost entirely of seedlings which had germinated since the hurricane. Paper birch dominated areas of exposed mineral soil although black birch and black cherry also occurred there. Noticeable was the absence of pin cherry, aspen, and gray birch.

TABLE VIII. Frequency of restocking on the Pisgah Tract, 1942

Species	High slopes	Low slopes	Total
Species most frequent on high slopes			
Paper birch	69	48	56
Red maple	42	23	30
Black cherry	42	16	26
Black birch	46	7	21
Species most frequent on low slopes			
Hemlock	35	55	47
Beech	12	27	21
Yellow birch	4	16	11
Infrequent species			
Red oak	..	..	3
White pine	..	..	3
Red spruce	..	..	1
Gray birch	..	..	1
Total	94	94	94

In this case where no logging followed the blowdown of old growth pine and hemlock, the following stand represents essentially a later successional stage than the preceding one, being characterized by hemlock and beech. In other words, the blowdown accelerated rather than set back successional development by felling the overstory and releasing the tolerant understory.

SUMMARY

Studies of natural restocking in and around the Harvard Forest, Petersham, Massachusetts, during the 10-year period following the hurricane of September 21, 1938, have yielded information on successional trends on hurricane blowdown areas. Four surveys of restocking were made in 1941-42 involving a total of 4,370 mil-acre quadrats. In addition, 14 permanent sample plots, mostly 0.1 acre in size, were tallied at intervals from 1940 through 1948.

Many factors apparently affect the composition of the new stand on a given area, prominent among them being: (1) soil type, (2) composition of the former stand, (3) advance growth present at the time of blowdown, and (4) whether the down timber was logged or not.

Where ample advance growth was present and no logging was carried out, the new stand is essentially a late-successional association composed of the released understory trees. Where advance growth is present but where the timber has been logged, the released understory trees are intermingled with pioneer species that have seeded in on the disturbed areas. Where little or no advance growth is present, pioneer associations exist.

Red oak and red maple are the characteristic dominant species on all sites although they are often outnumbered by pioneer species. White pine is characteristic of the sandy outwash soils, and is found in a suppressed state on the till soils. White ash and other mesophytes are found on the till soils, particularly on the imperfectly drained and the more fertile sites. The principal pioneer species are gray birch, pin cherry, and black cherry, but these are short-lived and will eventually disappear from the association. Pioneer species also include paper, black, and yellow birches which

are relatively long-lived and which will form part of the mature associations.

In practically every case, the character of the new stand was apparent within only two growing seasons of the hurricane. The absence of later successful invasion of seedlings is attributable in part to competition from growth already established, and in part to unfavorable environment in the blowdown areas.

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THE USE OF DISTANCE MEASURES IN PHYTOSOCIOLOGICAL SAMPLING[1]

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Introduction

A number of methods have been described in recent years which utilize spacing distances instead of fixed-area plots for the sampling of plant communities in compositional studies. All of these methods possess certain obvious advantages when compared to the standard plot techniques, since they all are more efficient in terms of results obtained per man-hour expended. They are faster, require less equipment and fewer workers, and are much more flexible, in that there is no need to adjust the sample size for the particular density of the vegetation type under study. The advantage in speed is particularly great, with savings of 90% or more commonly obtained. Currently, the main disadvantage of these distance methods lies in their unfamiliarity, which raises doubts as to their precision and limitations. The purpose of the present paper is to compare some of the methods, as used on three natural forests and an artificial random population, with respect to their relative accuracy and other characteristics.

In a stand of any plant community, the component individuls exist in a certain number, distributed over a certain area. This characteristic, called density, may be determined for each species separately, or for each life form (*e.g.*, trees) independently of species. In fixed-area plot sampling, a relatively small portion of the total area is examined, usually by means of a number of separate subsamples. In each of these subsamples, the density is determined directly by counting and the result expanded to total density per stand (or per acre) by use of the ratio between sample size and stand size. Instead of this idea of the number of plants per unit area, a more useful concept is the amount of area per plant, the *mean area* (M), which is the reciprocal of the density. When plant abundance is given as mean area, the way is immediately opened for the use of distance between plants as a measure of that

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abundance, since the $\sqrt{M}$ is a direct indication of the spacing of the plants. It follows that a measurement of the actual spacing in the field can lead to an accurate estimate of the mean area and the density. All of the distance methods so far proposed are based on this simple relation. They differ primarily in their choice of the distances to be measured so as to arrive at a correct determination of the actual spacing.

The actual number of individuals per unit area is only one of the characteristics of a plant community that may be measured and is frequently of lesser importance than certain other characteristics, especially when different stands of the same formation or type are being studied, all of which are relatively similar in absolute density. The same is true for measures of total dominance, such as the basal area of all trees per acre. This information may be of value in a timber cruise, or in other economic estimates, but is frequently of limited utility in basic phytosociological investigations. The use of extensive studies of many stands of related community types in a given region is coming to be recognized as the best approach to an understanding of regional vegetation, as opposed to the older procedure where an intensive study was made of one or a few "characteristic" stands. In such extensive studies, the use of a number of analytical characters on a relative basis, such as relative frequency, relative density and relative dominance, provides more useful information than that derived from the same characters on an absolute basis. Any sampling method, therefore, should be able to accurately provide such relative information in addition to the absolute values.

The distance measuring methods of community study have all appeared since 1947, when Cottam described the random pairs method for sampling forest trees. Subsequent investigations have been concerned with the use of distance either for the determination of density or for the study of the randomness of dispersion of the population. Skellam, in 1952, suggested that the distance between each individual in the population and its nearest neighbor might be used to study randomness, through a comparison of the observed distribution of such distances with those expected from theory. Cottam, Curtis, and Hale (1953) used the point-centered quarter method for measurement of density and a number of relative characteristics. They also reported certain properties of the distances between random points and closest individuals (point to plant) and of the distances between nearest neighbors (plant to plant). Hopkins (1954) compared the average distance between nearest neighbors with the average distance between random points and closest individuals as a means of measuring aggregation. This had been suggested independently by Moore (1954) who also used these measurements to determine densities. Clark and Evans (1954) also used the nearest neighbor distances in a study of aggregation. All of the methods have thus been used for density determination and some of them in addition have been used for the study of randomness. In view of the wide interest, it has seemed desirable to compare the characteristics of the methods under comparable conditions.

METHODS

Three forest communities and an artificial random population were each sampled by five methods—the closest individual, the nearest neighbor, the random pairs, the point centered quarter, and the quadrat. The three natural communities were first mapped by plane table and transit procedures so that each tree was accurately located and its species and basal area indicated on a map drawn to 1/192 scale (1/16 inch equals one foot). The three forest communities were chosen to represent a wide range in species complexity, tree size, and tree density. Peavey Falls Woods is located on the Menominee Indian Reservation in Shawano County, eastern Wisconsin. Jack Pine Woods is in Bayfield County, northern Wisconsin. Wingra Woods is located on the University of Wisconsin Arboretum in Dane County, southern Wisconsin. Details about species composition, density, and dominance of these stands are given in the tables. The Peavey Falls Woods map covered an area of 1.63 acres which contained 600 individuals. The Jack Pine Woods map covered an area of 0.48 acres containing 330 individuals. The Wingra Woods map covered an area of 5.37 acres which contained 543 individuals. A rectangular area was drawn in the center of the map large enough to include most of the mapped individuals, but with a border at least two trees wide between the edge of the rectangle and the edge of the map. This rectangular area was then divided by a 10 x 10 place grid into 100 equal sub-units. Within each sub-unit, 100 permanent sampling points were located by means of a random numbers table. The same sampling points were used for each method, and all data are based on a total of 100 sampling points for each method for each stand. No method of mutual exclusion was used in the location of the sampling points so that any tree could be, and in many cases was, sampled more than once with the same method. The populations on the maps were considered to be infinite.

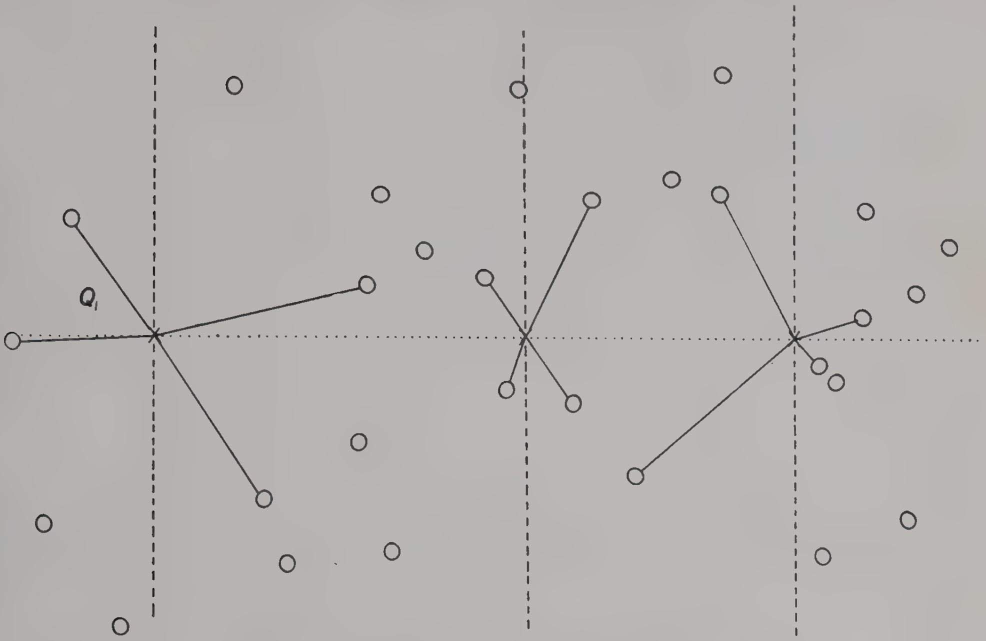

FIG. 1. Point to Plant Methods. X's are sampling points. Dotted lines are paced compass lines between points. For the closest individual method, distance is measured from the sampling point to the plant closest to it, regardless of direction (Q_1). For the quarter method, the area around the point is divided into four 90° quarters (dashed lines) and distance is measured from the point to the closest tree in each quarter. Solid lines on the figure represent measured distances.

The artificial random population of 1,000 individuals was the same as that used by Cottam, *et al.* (1953). No basal areas were available, since each individual was considered as a point in space. Sampling followed a stratified random system like that used on the natural communities.

Closest individual method. (Figure 1).—This is the simplest of the point to plant methods. The distance from the sampling point to the closest tree is measured, and the species and basal area of the tree are recorded. The mean of the distances from the sampling point to the closest individual has been found to equal 50 per cent of the square root of the mean area. This was demonstrated empirically by Cottam, *et al.* (1953) and theoretically by Morisita (1954). The average point to closest individual distance is therefore multiplied by a correction factor of 2.00 to convert it to square root of the mean area.

Nearest neighbor method. (Figure 2).—As used by Cottam, *et al.* (1953), the nearest neighbor distance is the average distance from each individual in the population to its closest neighbor. Many of the values are duplicates, since paired neighbors (which have each other as nearest neighbors) make up a significant portion of the total population. Hamming and Gilbert (1954) showed that 62% of the total number of individuals in a random population are in these isolated pairs. Clark and Evans (1955) confirmed this relationship for both artificial and natural populations. Morisita (1954) demonstrated that, in a randomly distributed population, the distance between nearest neighbors is equal to one-half the square root of the mean area. Using other symbols and terms, Clark and Evans (1954) independently arrived at the same conclusion. The latter investigators state that a random sample of the individuals in the population will also yield a mean distance equal to one-half the square root of the mean area. This is undoubtedly correct, but requires an additional explanation in connection with the present problem. Clark and Evans point out that in order to obtain a truly random selection of the individuals in the population, it is necessary to number all the individuals in the population and select the individuals to be sampled by lot. As an approximation, they recommend establishment of quadrats at random and measurement of the nearest neighbors of the individuals within the quadrats. Neither of these methods is satisfactory for the present purpose, since both of them are so time consuming that their use would destroy any advantage this method may have.

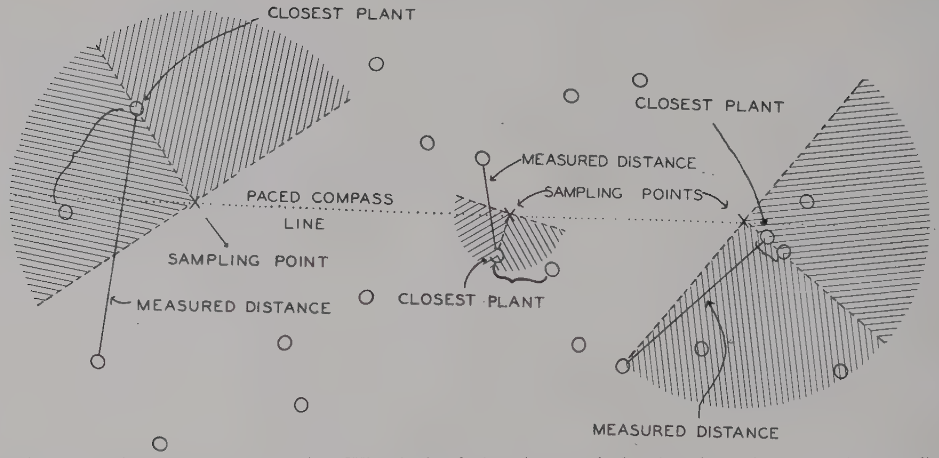

FIG. 2. Plant to Plant Methods. With both of the plant methods, the plant closest to the sampling point is located. Nearest neighbor distance is measured between the bracketed plants at each point. For the random pairs method, an angle of exclusion of 180° (shaded area) is erected with its vertex at the sampling point and its bisector extending through the closest plant. Distance is measured from the closest plant to the plant closest to it that is outside the angle of exclusion (solid line).

The method for tree selection used in the present study was to choose the individual closest to each sampling point (the same tree to which distance was measured in the closest individual method) and to use this tree as the tree from which distance to its nearest neighbor was measured. This does not provide the truly random sample called for by Clark and Evans, and does not yield the same results. In a series of artificial random populations, which were examined by a 100 per cent sample, it was found that the average distance between paired individuals was 37 per cent of the square root of the mean area while the average distance between non-paired neighbors was 66 per cent. A stratified sample, by the method outlined above, of one of these artificial populations showed that only 50 per cent of the distances measured were between paired neighbors, as opposed to the 62 per cent expected from a truly random sample of the individuals. Also, the distances between these paired individuals which were sampled was 47 per cent of $\sqrt{M}$ as opposed to the 37 per cent figure for all the paired neighbors on the population. The nearest neighbor method, as described, not only samples fewer of the paired neighbors than occur proportionately in the population, but tends to sample those paired neighbors that are far apart more often than those that are very close together. As a result, the average distance between individuals with the nearest neighbor method, as here used, is approximately 60 per cent of $\sqrt{M}$ instead of 50 per cent as in a 100 per cent sample. The use of a set of individuals chosen in this manner and their nearest neighbor distances involves multiplication of observed distances by a correction factor of 1.67 instead of the theoretical 2.0, to obtain the correct $\sqrt{M}$. The nearest neighbor method gave a sample of 100 distances and 200 trees for 100 sampling points.

Random pairs method. (Figure 2).—Considerable confusion appears to exist about the random pairs method and its uses and limitations. Some investigators have used it with success (Dimit and Russell 1954) but other workers have reported difficulties (Shanks 1954, Rice and Penfound 1955). The method is based on the use of an angle of exclusion to denote a series of pairs of plant individuals for further sampling of species, size and spacing distance. As originally described (Cottam and Curtis 1949) an exclusion angle of 160° was recommended but it was later shown (Cottam, *et al.* 1953) that the average distance between pairs was a linear function of the angle of exclusion for 0° to 260°. Since a 180° angle is most convenient in the field, its use is recommended. The actual distances obtained with the 180° angle should be multiplied by a factor of 0.80 to obtain the correct distance (Cottam and Curtis 1955).

As used here, the random pairs method involves the choice of the closest tree to each of the stratified sampling points, the erection of a 90° exclusion angle on either side of the line between the sampling point and the closest tree, and the selection of a second tree, outside of this total

180° angle, which is closest to the first individual. Basal areas and intertree distances are recorded, thus giving a sample of 100 distances and 200 trees for 100 sampling points.

Point-centered quarter method. (Figure 1).—This method is a very old one, having been used by the Federal surveyors making the original survey of government lands in the middle of the last century (Stearns 1949). As adapted for ecological use (Curtis 1950), each sampling point is considered the center of the four quarters (quadrants), with orientation given by the compass line of traverse. At each point, the closest tree to the point in each of the four quarters around the point is chosen as the sample. Distances are measured from the point to each of the four trees, and their species and basal areas recorded. The average of the four distances is equal to $\sqrt{M}$, as demonstrated empirically by Cottam, *et al.* (1953) and theoretically by Morisita (1954). Additional information of interest can be obtained by arranging the distances about each point in order, from the shortest (Q_1) to the longest (Q_4). It has been shown (Morisita 1954) that the Q_1 distance, which is the distance from any point to the individual nearest to that point, is equal to $0.5\sqrt{M}$ and is thus the same, on the average, as the distance between any individual and its closest neighbor. The Q_1 distance is identical to the closest individual distance as given above. The Q_2 distance is equal to $0.80\sqrt{M}$, the Q_3 to $1.12\sqrt{M}$, and the Q_4 to $1.57\sqrt{M}$, while Q_m, which is the average of Q_1 Q_2, Q_3, and Q_4, exactly equals $\sqrt{M}$. As used here, the point-centered quarter method gives 100 Q_m distances and 400 trees for every 100 sampling points.

Quadrat method.—The standard quadrat method involved the placement of a quadrat centered directly over each sampling point. The quadrats were equal to 4 times the population mean area in size, so they could be expected to contain 4 individuals on the average in a random population (Curtis and McIntosh 1950). For each quadrat, the species and basal area of each tree were recorded as well as the total number of trees. A sample of 100 points thus gave a variable number (approximately 400) of individuals.

For the natural populations, the importance value (Curtis and McIntosh 1951) was calculated for each species, considering each point as analogous to a quadrat for frequency determination. Relative densities and relative dominances were calculated in the usual way. It is important to realize that these importance values (the sum of relative values of frequency, density, and dominance) are independent of distances or absolute densities per unit area. For certain comparative studies where they may be of considerable interest, it is unnecessary to measure the distances at all, but such a practice is not recommended for most investigations.

RESULTS

Computation of density and dominance with the distance methods requires the determination of the following:

1. Mean distance. This is determined by adding all the distances in the sample and dividing this figure by the total number of distances.

2. Relative density and relative dominance. These are determined from the following equations:

$$\text{Relative density} = \frac{\text{Number of individuals of the species}}{\text{Number of individuals of all species}} \times 100$$

$$\text{Relative dominance} = \frac{\text{Total basal area of the species}}{\text{Total basal area of all species}} \times 100$$

3. Basal area per tree. This is determined by dividing the total basal area by the number of trees.

The mean distances are used to determine mean area and density per unit area. All other absolute measures are computed from the density per unit area figure. As has been stated in the section on methods, the mean distances obtained with each method, except the quarter method, must be multiplied by a correction factor, which is constant for the method, in order to arrive at the correct square root of the mean area. The quarter method gives the correct square root of the mean area directly. After correction, the distances are squared to give mean area, and the mean areas are divided into the unit area to give number of trees per unit area.

A comparison of the results obtained with the four distance methods and the quadrat method on the mapped stands and the artificial population is presented in Table I. After correction, the distances are all within 5 per cent of the actual square root of the mean area, and trees per acre are within 10 per cent of the actual values.

Total basal area per acre is obtained by multiplying number of trees per acre by the mean basal area per tree. Absolute values for number of

Table I. Comparison of results from the various methods with each other and with the population parameters

Method	Closest individual	Nearest neighbor	Random pairs	Quarter	Quadrat	Actual
			ARTIFICIAL POPULATION			
Distance	16.19 mm.	18.85 mm.	40.18 mm.	32.05 mm.	32.26 mm.	31.65 mm.
Corrected distance	32.38	31.48	32.14	32.05	32.26	31.65
Mean area	1048.46	990.99	1032.98	1027.20	1040.71	1001.72
			WINGRA WOODS			
Distance*	10.75	13.05	26.91	21.02	20.17	20.75
Corrected distance	21.50	21.79	21.53	21.02	20.17	20.75
Mean area	467.25	474.80	463.54	441.84	406.83	430.56
Trees/acre	93	92	94	99	107	101
Basal area per tree†	179.2	180.5	189.4	200.1	179.0	188.6
Basal area per acre‡	115.7	115.3	123.7	137.6	133.0	132.3
			PEAVEY FALLS WOODS			
Distance	5.21	6.80	13.68	10.58	11.07	10.89
Corrected distance	10.42	11.46	10.94	10.58	11.07	10.89
Mean area	108.58	129.05	119.68	111.94	122.54	118.69
Trees/acre	401	338	364	389	373	367
Basal area per tree	119.7	118.4	105.9	107.0	103.5	102.2
Basal area per acre	333.3	277.9	276.8	289.0	268.1	260.5
			JACK PINE WOODS			
Distance	3.93	4.80	10.52	7.77	8.22	8.00
Corrected distance	7.86	8.02	8.42	7.77	8.22	8.00
Mean area	61.78	64.32	70.90	60.37	67.57	64.00
Trees/acre	705	677	614	722	645	681
Basal area per tree	23.1	22.0	22.7	22.8	21.4	21.6
Basal area per acre	113.1	103.6	97.0	114.5	96.1	102.2

*Distances for the natural populations have been converted to feet.
†Basal areas per tree are in square inches.
‡Basal areas per acre are in square feet.

trees per unit area of any species, and basal area per unit area of any species are determined by multiplying the relative figures for density and dominance by total trees per acre to determine density, and by total basal area per acre to determine dominance. An alternative computation for basal area per acre for a species is to multiply number of trees per acre of the species by the basal area of the average tree of the species. Basal area of the average tree of the species is determined by:

$$\frac{\text{Total basal area of the species}}{\text{Total number of trees of the species}}$$

Either computation will produce the same result.

Since basal area per acre is determined by multiplying basal area per tree by number of trees per acre, and all absolute density values are determined from the figure for trees per acre, it is apparent that the accuracy of all absolute values is dependent in part upon an accurate figure for number of trees per acre. It follows that care should be taken to insure that the sample of distances is adequate, and that the measurements are made with accuracy.

The number of distances required to produce an adequate sample varies with the method employed. Table II shows coefficients of variation for the four methods on each of the populations. In all cases, except the nearest neighbor method for the Jack Pine stand, the coefficients of variation are similar for each method for all populations. Coefficients of variation are highest with the closest individual method and lowest with the quarter method. The fact that the quarter method gives the lowest coffiecient of variation is not surprising in view of the fact that each recorded distance is actually the mean of the four distances Q_1, Q_2, Q_3, and Q_4 for each point, and any large deviation of one of these distances at any point is likely to be compensated by an opposite deviation of the others.

A standard error of less than 10 per cent of the mean is considered satisfactory for most biological work. A more stringent requirement was placed on the distance measurements because these distances must be squared before density may be determined. It was desired that the standard error of the distance measurements be such that,

TABLE II. Variability of distances. Figures in bold-faced type are coefficients of variation. Figures in italics are number of distances required to yield a standard error of less than 4.65 per cent of the mean

	Closest individual	Nearest neighbor	Random pairs	Quarter
Artificial population..	49.5%	46.9%	32.9%	23.7%
	114	*102*	*50*	*26*
Peavey Falls Woods..	56.1	45.0	39.1	23.6
	146	*94*	*71*	*26*
Wingra Woods.......	54.3	46.3	36.2	28.8
	136	*99*	*61*	*38*
Jack Pine Woods.....	51.2	35.6	36.4	25.6
	121	*59*	*61*	*30*

when they were converted to densities, the plus or minus figures be within 10 per cent of the mean density. This condition is met with standard errors of the distances of 4.65 per cent or less. The figures in italics on Table II show the number of distances required to bring the standard error of the distances to 4.65 per cent of the mean distance. Less than 40 quarter distances are required, but more than 100 closest individual distances.

The adequacy of sampling of basal areas is determined by two factors: the number of trees encountered in the sample and the range and distribution of the sizes of the trees. Neither of these factors is greatly influenced by the method of sampling, except that the methods encounter a different number of trees per point, and those methods which measure the basal areas of only one or two trees per point will require four or two times as many points for the same adequacy of sample as is obtained with the quarter method, which measures four trees at each point.

The differences that may be encountered in sampling forests of this region are shown by a comparison of the two stands which differ most widely in basal area characteristics: Peavey Falls Woods and Jack Pine Woods. Peavey Falls Woods has many small hemlocks (*Tsuga canadensis*) which average 40 square inches in basal area. The next most common species is white pine (*Pinus strobus*), ranging in size from 50 to 1169 square inches basal area, with an average of about 200 square inches. Jack Pine Woods, on the other hand, is an even-aged stand of small jack pines (*Pinus banksiana*) in which the basal areas range from 12 (the lower limit mapped) to 45 square inches. Coefficients of variation for the basal areas per tree of these two stands were computed. The data were transformed by a square root transformation. Coefficients of variation range between 58 per cent and 66 per cent for the different methods in Peavey Falls Woods and between 17 and 18 per cent in Jack Pine Woods. The number of trees required to produce a standard error of the transformed data of less than 10 per cent of the mean is very uniform for the different methods in either stand, but approximately 10 times as many trees must be sampled in Peavey Falls Woods as in Jack Pine Woods. The number of points required in either case is less than that required for an adequate sample of distances. In almost all cases, a sample of sufficient size to give an adequate sample of distances will produce an adequate sample of basal areas as well.

It has been stated in the section on methods that, in some cases, relative values for frequency, density, and dominance as used in the calculation of importance values are adequate, and in such cases, distances need not be measured. Importance values for the three mapped stands are shown in Table III as computed for the four distance methods and the quadrat method. It can be seen that the five methods result in very similar importance values for all species. The only trend is a slight lowering of the importance value for the most common species in the methods having the largest number of trees per sample (quarter and quadrat methods). This is due to the fact that relative frequency for the common species drops as number of trees per sample is increased, with a corresponding rise in relative frequency for the species of medium occurrence.

TABLE III. Importance values (sum of relative frequency, density, and dominance) obtained for the natural populations

Species	Closest individual	Nearest neighbor	Random pairs	Quarter	Quadrat
			PEAVEY FALLS WOODS		
Tsuga canadensis....	128	120	126	116	116
Pinus strobus.......	99	96	96	84	94
Acer rubrum........	34	43	39	57	50
Acer saccharum.....	28	21	26	31	26
Betula lutea.........	4	9	5	6	9
Betula papyrifera....	—	2	2	1	2
Quercus borealis.....	5	2	2	2	1
Ostyra virginiana....	2	2	2	2	2
Abies balsamea......	—	—	1	—	1
			WINGRA WOODS		
Quercus borealis.....	218	213	212	207	209
Quercus alba........	55	61	64	63	61
Quercus velutina.....	14	15	16	19	19
Carya ovata.........	13	11	8	10	12
			JACK PINE WOODS		
Pinus banksiana....	300	299	300	294	297
Betula papyrifera....	—	2	—	6	3

The rare species are unaffected, but fluctuate due to the inadequacy of the sample of these species.

Discussion

Since all the distance methods here discussed are based on the same general principle, it is to be expected that they would all yield similar results if an adequate sample is used. The data presented indicate that this is the case, and the problems concerned with selection of method are not concerned with relative accuracy. All are equally accurate if an adequate sample is used. As regards personnel and equipment, the methods are also about equal. The basic requirements are a tape for measuring distances and basal areas, and a compass. All of the methods can be used by a single individual without undue loss of efficiency, but a team of two in which one man acts as recorder is probably more efficient as well as more accurate, since a single individual finds that the chief limitation to his speed is the necessity for stopping and recording the data. An additional instrument that greatly increases speed is a good optical range-finder. Such an instrument is available which has a 6 inch base and is accurate to within half a foot at 40 feet. The accuracy of the instrument probably exceeds the accuracy of a tape in many forest stands, where the presence of underbrush makes the measurement of distances between trees with a tape difficult at times.

Evaluation of the merits of the methods must be based on other criteria than accuracy or personnel. Probably the most important factor is the time required to obtain an adequate sample. It is obvious that the method requiring the measurement of a single tree and a single distance at a point requires less time per point than the quarter method, which requires the measurement of four distances and four basal areas at a point. The greater amount of time required per point with the quarter method is, however, more than balanced by the smaller variability of the results with this method, which results in the necessity for fewer points. No single answer can be given to the question of how many points are required to give an adequate sample with the different methods. This depends on the data to be taken and the nature of the stand. The number of points required to yield adequate figures may be different for each phytosociological character to be determined. The characteristics of the methods will therefore be considered in relation to their ability to measure density and basal areas.

Absolute density is based on the distance measurements, and the results indicate that the quarter method requires the fewest points. The variability in the case of distance measurements is a characteristic of the method, when populations with an approximately random dispersion are used. Of the two methods measuring two trees at a point but only one distance, the random pairs method with a 180° angle requires fewer points and is preferable for that reason. The closest individual method is the most variable of all and is not recommended for distance determinations, although it has uses, in conjunction with some of the other distance methods, is measuring randomness or aggregation.

The above discussion is based on theoretical considerations and presupposes a random, or at least an objective, location of the sampling points and a population of individuals that has a spatial distribution approaching randomness. There are also some subjective considerations that become important in the field. The usual method of locating the points at which samples are taken is to pace a compass line. Subjective bias enters in the process of walking the compass line. Repeated sampling of the same stands with different investigators indicates that some individuals have a tendency to subconsciously place the sampling points so that large or unusual trees occur in the sample more commonly than they occur in the stand. This may be the case in spite of the fact that a pre-determined compass line and a predetermined number of paces between points were used. This bias is relatively unimportant with most workers and is probably never deliberate, but it does exist. It is mentioned here because it has a bearing on the choice of method. Bias of this sort will influence the data obtained by the closest individual method more than the others, since only one tree at a point is measured, and subconscious deviation form the compass line toward a single tree is relatively easy. It is much more difficult to place a point, consciously or otherwise, so that two trees or four trees at a point can be predetermined. Distances are even more subject to the influence of this bias than are tree species when the closest individual method is used, but the mean distance from the point to trees in four quarters is affected very little if at all.

Basal Areas

The adequacy of the sample of basal areas appears to be dependent almost entirely on the number of trees sampled, and the number of trees required to give an adequate sample is a character of the population, not of the method. Number of trees required will depend on the nature of the stand, with those stands having trees of fairly uniform size requiring fewer points than stands in which trees of all sizes occur. Here the choice of method is primarily a matter of deciding whether it is more economical of time and effort to measure many points with one or two trees, or fewer points with four trees per point. The subjective bias mentioned above is an argument in favor of the quarter method, and the possibility that the presence of a species may influence the species or size, or both, of the tree nearest it is an argument opposed to the use of the nearest neighbor method.

This discussion has so far concerned itself with a comparison of the four distance methods and the quadrat method. There remain several important considerations that are common with all distance methods, and many of them apply to the quadrat method as well. Perhaps most important is the necessity for using the mean distance and mean basal area of the data from all the points to determine absolute density and dominance. The distance methods should be considered as consisting of two samples, a sample of distances and a sample of tree species and basal areas. This point has led to some confusion in the literature. When density per acre and basal area per acre are computed independently for each point, the results, as Shanks (1954) has pointed out, may be greatly in error.

Two different errors are introduced by this procedure. The first is due to the fact that distances must be squared before density may be computed. The methods used in this paper are based on squaring the mean distance, and the correction factors given apply only when this procedure is followed. Squaring the individual distances and then computing the mean of these squared distances will always result in a higher figure than the square of the mean of the same distances, unless all the original distances are equal.

The second source of possible error is the extreme variability introduced by multiplying the number of trees per acre by basal area per tree at each point. An attempt to correlate basal area per point with mean distance per point for the quarter method showed that distance and basal area at each point are independent of each other in the range of forest types studied, as would be expected from biological considerations. The chance combination of a short distance and large basal area at a single point will result in a wide range of basal areas per acre, if the points are considered one by one. For example, treatment of the Peavey Falls quarter data as separate samples results in a range of basal areas per acre from 29 square feet to 4384 square feet.

It must be pointed out, however, that the values for basal area per tree and density per acre are independent and are multiplied by one another to obtain basal area per acre for the stands. This means that basal areas per acre are less reliable than either of the two components when considered separately. In some cases, errors in the two compensate for one another, as in the case with the 180° random pairs data for Jack Pine Woods (Table I). Here the number of trees per acre is low, and the basal area per tree is high, with the result that the two combined produce an answer for basal area per acre that has a smaller percentage error than either of the original figures. On the other hand, the quarter data for the same stand show too many trees per acre and too large a basal area per tree with the result that, although the two components are within 10 per cent of the actual values, the basal area per acre value is in error by approximately 12 per cent.

A second consideration that is important with all methods, including the quadrat method, is the necessity for objectivity in the selection of the sampling points. This is best accomplished by the introduction of some randomization technique. The method of point selection recommended for use with the distance methods is one of paced compass lines, and an element of randomness may be introduced by varying either the number of paces or the direction of the compass line according to a pre-determined system involving the use of random numbers. Other more rigorous techniques for randomization are available, but they are so time consuming that their use would nullify one of the principal advantages of the distance methods—speed. It is important that whatever technique for the selection of sampling points is used, it must be followed with extreme care. Any relaxation of the controls on point selection allows the possibility of subjective bias.

A final consideration in connection with the distance methods is their behavior when populations with a considerable degree of aggregation are sampled. Aggregation of total trees in forest stands is usually so slight that it does not present a serious problem, although individual species are frequently non-random. A complete treatment of the problem of aggregation is beyond the scope of this paper, but it should be mentioned that when trees are noticeably clumped, with open spaces between the clumps, none of the distance methods as here described will give an accurate density.

Aggregation tends to increase distances obtained with the closest individual, random pairs, and quarter methods, and tends to decrease the distances obtained with the nearest neighbor method. Several methods for measuring aggregation have been published, but no methods that give accurate densities for such populations are available. Quadrat data in aggregated stands are so variable that the number of quadrats required is almost impossible to attain. At the moment it must be said that we know of no good method for measuring the density of aggregated populations.

Summary and Conclusions

Four distance methods, including two point-to-plant and two plant-to-plant methods, were used on three mapped stands and artificial population. The data were compared with results obtained with the quadrat method, and with the known population parameters. It was found that all the distance methods were capable of yielding accurate results when an adequate sample was used, but that the size of an adequate sample varied with the method.

The closest individual method has the advantage of simplicity. Only one tree and one distance are measured at each point. An additional advantage is that the mathematical characteristics of the method have been worked out, and the observed distance need only be multiplied by a factor of 2.0 to give square root of mean area. The disadvantages of the method are the extreme variability of the results, which necessitates the sampling of many points before an adequate sample is obtained, and the susceptibility of the method to subjective bias.

The nearest neighbor method gives less variable results than the closest individual method, but still requires a larger number of sampling points than either of the other methods. It, too, is simple, requiring only the location of the tree nearest the sampling point, and the measurement of the distance from that tree to its nearest neighbor. The results obtained with this method do not agree with the results based on mathematical theory, largely due to the fact that the method of sampling does not provide a random sample of the trees, but rather tends to under-sample trees that are close to one another. This results in a correction factor of 1.67 rather than the theoretical 2.00. The method does, however, yield consistent results in all stands in which it has been used.

The random pairs method with an 180° angle of exclusion is less variable than the two previously discussed. It has been more widely used than the other methods. One disadvantage is that the mathematical theory behind the method has not been worked out.

The quarter method gives the least variable results for distance determinations, provides more data on tree species per sampling point, and is least susceptible to subjective bias. The mathematical characteristics are known. It requires no correction factor, the mean of the distances equalling the square root of the mean area. The apparent disadvantage of requiring more time per point is compensated for by the necessity for sampling fewer points.

It is the opinion of the authors that the quarter method is, in most respects, superior to the other distance methods studied, and its use is recommended.

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USES OF UNDERGROWTH PLANT SPECIES IN FORESTRY[1]

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Introduction

There is no doubt that forest undergrowth can be put to practical use in forestry, not only for the simple purpose of stand description but also for the interpretation of successional trends, regeneration possibilities, site quality, and so forth. The chief obstacle to the fuller use of the minor species is lack of knowledge about them—their distributions, habits, tolerances, and hence the significance of their presence or absence at any particular place. For this reason it has been common practice when attempting to make some use of the forest flora to ignore the strictly ecological approach. In the study of forest site types, for example, the usual method adopted has been to search for recurring patterns of plant species in the hope that these can be be related to the occurrence and growth of particular forest types, and although satisfactory results have apparently been obtained in some instances, confusing or negative results have been obtained in others, with the result that plant indicators have acquired a bad name. It would be foolish to condemn the concept because it turns out to be less simple than at first suspected; the obvious need is for a more critical approach, and a closer study of the forest plants. It is safe to say that as more is learned of the ecology of the individual species, the more they will be found useful for various purposes. The present article outlines a method by which some of the more obvious "indications" of plants may be utilized in forestry.

The basic factors on which life depends are light, warmth, moisture, and nutrients, and it is the variability of these over the surface of the earth that is primarily responsible for the variability of plant and animal communities. The study of the ecology of a natural community consists largely of an analysis of the roles played in community organization by the basic factors, with particular attention to those which are believed to be limiting, as for example, temperatures in the arctic and moisture in desert regions. Unfortunately, it is not always possible to appraise directly the quantity and quality of the basic necessities of life in a given situation, and recourse to indicators is the only solution. The forester, interested in an assessment of moisture, nutrients, and radiant energy in relation to forest stands, can select from a wide choice of indicators: topography, humus layer, soil profile, geological parent material, and flora, to name the most obvious. All these, and many others, both condition and reflect the workings of the basic factors within the forest-environment whole. Each can furnish valuable clues to an understanding of the whole, yet none considered alone is sufficient to provide a fully reliable picture.

The writer does not intend to make a case for the exclusive use of plant indicators either to solve the problems of site classification or to guide the forester in silvicultural practices. The important point is that the alternative abiotic indicators, those collectively known as physiographic features, while possessing certain unique characteristics such as relative stability (advantageous or disadvantageous for particular purposes), are not necessarily more reliable nor easier to interpret than the flora. It is often as difficult to read the meaning of soil profiles as of plant communities, and furthermore, considerable back-breaking work is required before the former can be examined. It is obviously to the forester's advantage to learn what he can from the forest plants.

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Development of a Generalized Descriptive Scheme

No system for describing stands in general terms is available for the practicing forester in the southern boreal forest ("B.18. Mixedwood Forest Section," Halliday 1937) of Manitoba and Saskatchewan (Fig. 1). The methods described hereunder were developed primarily in an effort to find a satisfactory way of describing the forest vegetation, and were then modified as an aid to site studies. Although in this district only eight tree species are involved—white spruce (*Picea glauca*),[3] black spruce (*Picea mariana*), jack pine (*Pinus banksiana*), fir (*Abies balsa-*

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[3] Nomenclature of the higher plants is chiefly that of Fernald (1950), and for the mosses that of Grout (1940). Where other nomenclature is used, authorities are given only the first time that the names appear in table or in text.

mea), tamarack or larch (*Larix laricina*), aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), paper birch (*Betula papyrifera*)—their combinations result in a considerable number of cover types. Due to the prevalence of fire, most of the types are transitional. Generally speaking, however, they can be sorted out according to their status in one of two successional trends, either toward a white spruce (or white spruce and fir) type, or toward a black spruce type, although even these more stable communities are variable in composition and therefore afford no fixed standard to which the various seral communities can be related. It seemed advisable to work out an empirical descriptive method which could be applied to every stand found in the field, not relying on the principle of succession except as it served an interpretive purpose.

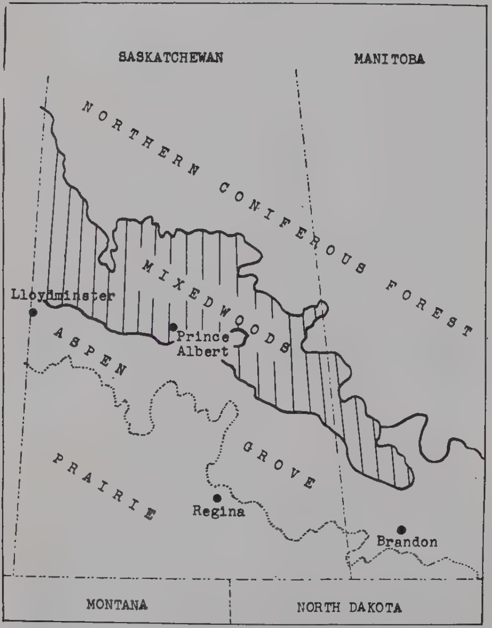

Fig. 1. Map showing location of the "Mixedwoods" section (southern boreal forest) in Saskatchewan and Manitoba.

The attribute of vegetation which lends itself most readily to description is physiognomy (Du Rietz 1931, Dansereau 1951) and a comparison of the structure of the forest undergrowth in various stands suggested one very helpful approach. Where sites are neither extremely dry nor extremely moist, the undergrowth of pioneer forest stands (of poplar, birch or even pine in some places) characteristically shows a high proportion of tall shrubs and/or tall herbs. In marked contrast is the clean forest floor under pure stands of spruce or spruce-fir, where mosses and low herbs are characteristic. If a list of the forest flora from non-extreme sites is divided into three groups on the basis of height alone as follows—tall shrubs and herbs (higher than 1m and 3 dm, respectively), medium shrubs and herbs (3 dm to 1 m, and 1 to 3 dm), low herbs and mosses (generally lower than 1 dm)—then the species in the tall and low groups are precisely those which stand out in deciduous forest (poplar and birch) stands and in coniferous (chiefly spruce) stands, respectively. The middle group cannot be related so specifically to cover-type preference, its species characterizing many kinds of stands.

The principal factor controlling the structure of the undergrowth is light, for although temperature, root competition, litter accumulation, and other soil characteristics exert a subsidiary effect, their main influence is on composition rather than on stratification. A poplar canopy allows much more light to penetrate to the forest floor than does a spruce canopy, consequently tall shrubs are able to flourish under the former but not under the latter forest. In a comparable way, an open

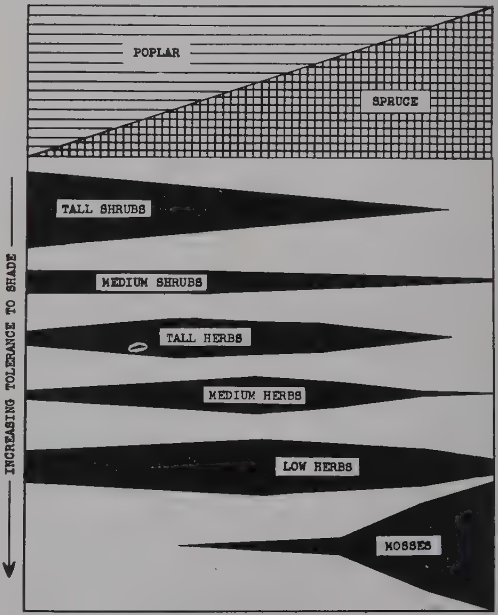

Fig. 2. The relative cover-abundance of undergrowth strata in mature stands of poplar, poplar-spruce, and spruce. (Data from quadrat studies in 20 representative stands.)

stratum of tall shrubs may allow tall herbs to survive, while a dense stratum eliminates all but the most tolerant. It is a fairly sound generalization that the relative height of the forest undergrowth species bears an inverse relationship to tolerance, since plants of low stature must be adapted to shade in order to survive. For example, the series: *Corylus cornuta* → *Aralia nudicaulis* → *Cornus canadensis* → *Calliergonella schreberi* (tall shrub → tall herb → low herb → moss) is clearly one of increasing tolerance to shade.

In order to illustrate the change in vegetative structure with increasing shade, an analysis was made of the comparative cover-abundance of the shrub, herb, and moss layers in stands representative of the successional series: poplar → poplar-spruce → spruce-poplar → spruce. The data were drawn from 400 milacre quadrats examined in 20 forest stands located on fresh to moist sites. Figure 2 shows the calculated percentage of total cover that the various layers contributed in this particular sample.

Note that the percentage of cover contributed by tall shrubs decreases steadily from poplar through mixed woods to spruce stands, while the percentage of cover contributed by mosses rises abruptly as mixed stands change to spruce. Note also that the cover-abundance of tall herbs is inversely related to that of tall shrubs in the poplar and poplar-spruce communities, reaching a high point in the latter. As poplar forest grades into spruce, medium shrubs decrease slowly and only a few (for example, *Viburnum edule* and *Ribes* spp.) are persistent where light intensities are low. Herbs of medium height have their best development in mixed stands. The low-herb stratum is strong in all communities, particularly in the mixed; its conspicuousness in spruce stands is due to the absence of the higher herb and shrub strata which tend to conceal it elsewhere.

A second feature useful in describing stands is found in the relationship between the forest plants and the soils which support them. In so far as single soil factors can be separated from the environmental complex and treated as "causes," soil moisture is probably the most important determinant of growth, and variations in moisture regime are always reflected in variations of the vegetation. In 1949, after two years of study in the southern boreal forest a table was drawn up ranking the forest species on a four-point moisture-preference scale (Rowe 1950). Subsequently, additional observations under various conditions of physiography and competition led to a partial revision of the table, and to the use of five moisture groupings: Dry (including Very Dry), Fresh, Moist, Very Moist, and Wet. The picture which has emerged of the moisture preferences of common forest species, relative to one another, provides a means of judging the moisture relations of particular stands.

Using these two features of vegetation, structure and moisture-preference, it is possible to characterize every forest stand with a descriptive epithet which conveys considerable information on density and successional status. Mention of the "dry, low grass-and-herb type" immediately calls to mind the open, limby stands of pine or white spruce which pioneer on excessively drained soils, just as the "moist moss type" suggests the dense, comparatively stable stands of spruce or spruce-fir on lower slopes and clay flats. When describing stands in this generalized manner, the names of the dominant trees are always included.

Note that in this scheme the characterization of stands according to structure of the undergrowth stresses the physiognomy that is evident to the observer. Thus, a "tall shrub type" may actually include tall-herb and low-herb strata, although these may not be mentioned because they are not readily seen. But where two or more strata are conspicuous, the description is expanded to include them, as for example, "the moist, tall shrub and moss type" (of pine forest).

The Vegetation Table

As an aid to more exact descriptions of plots and stands, particularly in the forests of the Riding and Duck Mountains, a field sheet was prepared on which the common forest species were located with reference to height on one coordinate axis and to moisture preference on the other. In use, the investigator checks off the plant species which occur on the area being studied, noting as well the prominent stratum or strata which contribute to the physiognomy or "look" of the stand. Notes on relevant environmental features (soil, aspect, topographic position, etc.) are also taken. Table I shows the vegetation part of the field sheet, as revised after one summer's use, with the relationship of tree species to moisture gradient indicated at the top of the page.

It should immediately be emphasized that the position occupied by each species in the table does not represent its only possible niche in natural communities. Consider the vertical scale: from top to bottom of the page are listed tall shrubs (more than 1 m tall), medium shrubs (3 dm to 1 m tall), tall herbs (more than 3 dm tall), medium herbs (1 to 3 dm tall), low shrubs and herbs (less than 1 dm tall), and the mosses and lichens. Obviously, there are numerous plants which can take their places, according to growing conditions, in

TABLE I. Vegetation table for the southern boreal forest

The species are arranged by strata in the vertical dimension and by moisture preference in the horizontal dimension. Species having little indicator value so far as moisture is concerned are in italics, and species characteristic of coniferous types are marked with an asterisk

	Very Dry and Dry Forest	Fresh Forest	Moist Forest	Very Moist Forest	Wet Forest
	xerophytic species	xero-mesophytic species	mesophytic species	meso-hydrophytic species	hydrophytic species
Vegetation Strata	←	Pinus banksiana	→	←	Larix laricina →
	←	—	Picea glauca	—	→
	←	—	Betula papyrifera	—	→
		←	—	Populus balsamifera	→
			←	Picea mariana	→
	←	—	Populus tremuloides	—	→
		←	—	Abies balsamea	→
Tall Shrubs (1 meter plus)	Alnus crispa Elaeagnus commutata Salix humilis Shepherdia canadensis	Amelanchier alnifolia Corylus cornuta Prunus pensylvanica Prunus virginiana	Acer spicatum Sorbus decora Viburnum trilobum	Acer negundo Cornus stolonifera Salix bebbiana Salix discolor	Alnus rugosa Salix petiolaris Salix pyrifolia
Medium Shrubs (3 dm. - 1 m.)	*Hudsonia tomentosa Juniperus communis	Diervilla lonicera *Rosa acicularis* Symphoricarpos albus Symphoricarpos occidentalis *Vaccinium myrtilloides	Lonicera dioica var. glaucescens	*Ledum groenlandicum Lonicera involucrata Lonicera villosa var. solonis Ribes glandulosum Ribes hirtellum Ribes triste Rubus idaeus Viburnum edule	*Andromeda polifolia Betula glandulosa *Chamaedaphne calyculata *Kalmia polifolia Rhamnus alnifolia Ribes hudsonianum Ribes lacustre Spiraea alba
Tall Herbs and Grasses (3 dm. plus)	Agastache foeniculum Anemone cylindrica Hedysarum alpinum var. americanum Hieracium canadense Lathyrus venosus Lilium umbellatum Pursh. Potentilla arguta	Agropyron subsecundum (Link) Hitchc. Anemone riparia Apocynum androsaemifolium *Aralia nudicaulis* Chamaenerion spicatum (Lam.) S. F. Gray Disporum trachycarpum S. Wats. Lathyrus ochroleucus Sanicula marilandica Thalictrum venulosum	Achillea sibirica Aquilegia canadensis Osmorhiza longistylis Solidago lepida	Anemone canadensis Aster umbellatus var. pubens Calamagrostis canadensis Cinna latifolia Heracleum maximum Pteretis pensylvanica Solidago gigantea Thalictrum dasycarpum Urtica gracilis	Arnica chamissonis Less. Aster junciformis Aster puniceus Cirsium muticum Eupatorium maculatum Glyceria borealis Impatiens capensis Petasites sagittatus Petasites vitifolius Sium suave
Medium Herbs and Grasses (1 - 3 dm.)	Achillea millefolium Aster laevis Astragalus alpinus Astragalus striatus Erigeron glabellus Castilleja rhexifolia Rydb. Comandra pallida Elymus innovatus Beal. Equisetum hyemale Gentianella amarella (L.) H. Sm. Habenaria bracteata Heuchera richardsonii Melampyrum lineare Oryzopsis asperifolia Poa interior Rydb. Polygala senega Rudbeckia hirta Solidago nemoralis Zizia aptera	Aquilegia brevistyla *Aster ciliolatus* Corallorhiza maculata Corallorhiza striata *Galium septentrionale* R. & S. Prenanthes alba *Schizachne purpurascens* *Smilacina stellata* Vicia americana Viola rugulosa	Bromus ciliatus Mertensia paniculata Osmorhiza obtusa Petasites palmatus	Dryopteris cristata Dryopteris disjuncta Dryopteris spinulosa *Geocaulon lividum Habenaria hyperborea Lysimachia ciliata Poa palustris Valeriana septentrionalis	Caltha palustris Equisetum arvense Equisetum pratense Geum macrophyllum Geum rivale Lathyrus palustris Mentha arvensis Parnassia palustris var. neogaea Senecio pauperculus Stachys palústris
Low Herbs and Grasses and Shrubs (Less than 1 dm. tall)	Antennaria campestris Antennaria petaloidea *Arctostaphylos uva-ursi Danthonia spicata Houstonia longifolia Festuca ovina Juniperus horizontalis *Lycopodium complanatum Oryzopsis pungens Polygala paucifolia *Sibbaldiopsis tridentata (Solond) Rydb.	Anemone quinquefolia Corallorhiza trifida *Fragaria virginiana* *Lycopodium obscurum *Maianthemum canadense* var. *interius* Pyrola asarifolia Pyrola secunda	Carex deweyana *Coptis groenlandica Corallorhiza trifida Cornus canadensis Fragaria vesca *Goodyera repens *Linnaea borealis var. americana Lycopodium annotinum Moehringia lateriflora (L.) Fenzl.	Circaea alpina *Equisetum scirpoides Galium triflorum *Gaultheria hispidula *Habenaria obtusata *Habenaria orbiculata *Listera cordata Mitella nuda *Moneses uniflora *Ranunculus lapponicus	Carex capillaris *Carex disperma Carex gynocrates Chrysosplenium ioense *Drosera rotundifolia Galium trifidum Ranunculus abortivus *Rubus acaulis *Rubus chamaemorus *Smilacina trifolia

	Very Dry and Dry Forest	Fresh Forest	Moist Forest	Very Moist Forest	Wet Forest
	xerophytic species	xero-mesophytic species	mesophytic species	meso-hydrophytic species	hydrophytic species
	Solidago hispida Spiranthes gracilis Vaccinium caespitosum Viola adunca		Monotropa uniflora *Pyrola virens Rubus pubescens *Trientalis borealis *Vaccinium vitis-idaea var. minus *Viola renifolia		Stellaria longifolia *Vaccinium oxycoccus Viola nephrophylla Viola palustris
Mosses and Lichens	Ceratodon purpureus *Cladonia rangiferina (L.) Web. Polytrichum piliferum	Brachythecium salebrosum Polytrichum juniperinum Rhytidiadelphus triquetrus	*Calliergonella schreberi *Dicranum rugosum Eurhynchium strigosum Eurhynchium diversifolium Peltigera spp.	*Hylocomium splendens *Hypnum crista-castrensis Thuidium recognitum	Aulacomnium palustre Camptothecium nitens Climacium americanum Drepanocladus uncinatus Mnium cuspidatum *Sphagnum spp.

more than one of these arbitrarily defined strata. The aim has been, however, to make the scale conform as closely as possible to the average physiognomy of the vegetation as observed in numerous forest stands throughout the eastern part of the Mixedwood forest section, and in most cases it has not been difficult to decide where any given species should be placed. More importance has been attached to the position of the vegetative foliage than to the flowering parts, and species such as *Elymus innovatus, Aster ciliolatus,* and *Mertensia paniculata,* which in flowering extend into the tall herb layer, are nevertheless ranked as medium herbs.

The position of each species relative to the horizontal moisture-preference scale is not meant to be interpreted in a hard and fast way, either. Plants of wide tolerance may be found in all sorts of communities, from dry to wet sites. However, most of the species exhibit a preference for one moisture regime (their "apparent optimum") over others, reflecting this preference in greater abundance and vigor, and it is expedient here to classify each according to the moisture column of closest fit. Intensive studies would make possible the subdivision of the moisture-preference classes as the finer responses of species relative to one another were distinguished, but for present purposes a five-point division of the moisture gradient is considered adequate.

The sampling unit in forestry work is usually a one-tenth or one-fifth-acre plot. On such limited areas, particularly when cover type and site conditions are relatively homogeneous, it has been found from quadrat studies that 40 to 50 species of minor plants are usually present (plus a number of rarer bryophytes and lichens which are not considered here). When these species are checked off on the table, a certain scatter-pattern is obtained depending on the nature of the overstory, successsional stage of the community, and the moistness of the site. It is often quite apparent from the presence pattern thus obtained that the weight of the community is concentrated in a particular part of the table, and this facilitates the characterization of stands by physiognomy and moisture regime.

Description of Forest Vegetation

The task of describing vegetation is very difficult. The investigator is confronted with the fact that no two stands are exactly alike; variability due to vegetational development and site differences occurs on every hand. Uusually the best that can be done is to describe selected "representative" stands, fully aware at the same time that no one will encounter in the field the exact conditions described.

Actually, a more useful description is a general one which indicates the probabilities of certain plants entering into the constitution of the vegetation in response to environmental variations. The vegetation table just described is an approach along these lines. It attempts to come to terms both with the important fact that a segregation of species occurs in relation to gradients of light and moisture, and with the corollary that ecologically similar species may replace one another on equivalent sites. The table may be interpreted therefore as a generalized description of many forest communities in the area studied. It suggests in a very broad way what may be expected so far as floristic composition is concerned under various degrees of crown closure and soil moisture.

One important qualification is necessary. The table places together all species which are somewhat similar in height, growth habit, and moisture preference, but this does not mean that they are necessarily ecological equivalents or even that they are found together in nature. To further refine the table for descriptive purposes, it would be necessary to mark those species which commonly occur together, thus suggesting more exactly the probable composition of communities under particular conditions of cover type and site. A rather broad division has been made in Table I by marking with an asterisk those species which are largely confined to coniferous forests.

Groups of species which consistently hold together are known as "synusiae" when their members belong to the same vegetational layer, or as "unions" (*sensu* Daubenmire 1952) when they belong to various layers. An example of the former is the *Cornus-Linnaea* synusia of moist spruce forests, consisting typically of the following low herbs: *Cornus canadensis, Linnaea borealis* var. *americana, Pyrola virens, Rubus pubescens, Trientalis borealis,* and *Viola renifolia.* An example of the latter is the *Corylus-Aralia* union of fresh poplar forests, in which species of several strata are included: *Corylus cornuta, Prunus virginiana, Aralia nudicaulis, Viola rugulosa, Lathyrus venosus, Galium septentrionale, Aster ciliolatus, Oryzopsis asperifolia, Fragaria virginiana,* and *Maianthemum canadense* var. *interius.* The possibility of characterizing stands by their synusiae or unions is a problem which will not be discussed here, as the chief concern of this article is to outline a more general descriptive scheme.

The vegetation table also indicates something of the developmental trends in forest communities. The common line of succession from poplar or pine to spruce or spruce-fir is marked by a diminution of light on the forest floor. As previously mentioned, the pioneer communities are characterized by an open canopy which allows tall shrubs and tall herbs to flourish beneath (provided that moisture is adequate). The more advanced communities—the white spruce, spruce-fir or black spruce—with their closer canopies make conditions unsuitable for survival of all except the most tolerant undergrowth: the low herbs and mosses. With some exceptions then, which are mentioned below, the top half of the table contains the species characteristic of pioneer open forest types, while the lower half contains those species characteristic of the coniferous types which stand further along in the successional series. The exceptions occur mainly in the Dry and Wet columns, and many of the low species which "prefer" these extremes of site moistness appear to be intolerant of much shade. For example, *Arctostaphylos uva-ursi* and *Sibbaldiopsis tridentata,* both low shrubby plants, are often found forming a ground carpet in dry open pine types, but they are absent or at least very rare wherever shade is intense. Other exceptions to the generalization are exemplified by the tolerance to shade of some medium shrubs (*Viburnum edule* and *Rosa acicularis*) and of some tall and medium herbs (*Aralia nudicaulis* and *Petasites palmatus*).

The most tolerant herbs of the forest are those listed as low herbs in the Fresh, Moist and Very Moist columns. Some of these species occur in communities of poplar or pine where they grow under the taller shrubs and herbs, and their prominence in the denser coniferous stands is a result of the shading out of the higher species which concealed them in the earlier successional communities. Figure 2 illustrates this very well. On the other hand, some of the low herbs show a high fidelity to spruce and fir stands only, and these characteristic species form a well-defined synusia, usually associated with a ground cover of feather mosses.

The mosses are the most tolerant of all species, and successional development from the more or less open pioneer stands to the close coniferous forest is marked by an increase in importance of this lowest layer. Mention should here be made of the special forest floor which is distinctive because of the virtual absence of any undergrowth species. This is the "needle cover" type, maintained under densely stocked (usually young) coniferous stands where both shade and root competition are intense (Moss 1953).

It is worth pointing out that the prominent stratum of the undergrowh in mixed and coniferous stands is frequently a good index of stand density, and in many instances it is possible to interpret the presence of a pronounced shrub stratum as indicative of an understocked forest, and the presence of needle cover or moss carpets as indicative of overstocking.

Forest Communities

A short description of some of the commoner forest community types which occur in the eastern part of the southern boreal forest ("B.18 Mixedwood" forest section) is next presented, using the moisture-physiognomy scheme. The series of communities, from those with a shrub layer to those with a moss layer prominent, are taken up in turn under each moisture class, and brief mention is made of some of the typical species participating. Intermediate types, although they are common, are not mentioned.

(1) The Very Dry and Dry Series of forests, occurring on excessively drained soils, are characterized chiefly by low grass-herb-shrub vegetation under jack pine or white spruce. Examples are the low heath-and-lichen (*Arctostaphylos-Cladonia*) pine types on siliceous soils, and the

park types (*Festuca* and *Agropyron*) of white spruce on calcareous gravels and sands, these latter representing recent invasions of prairie by the forest. On slightly less dry sites, a few examples of tall shrub types have been found, featuring *Alnus crispa* or *Salix humilis* under jack pine.

Possibly the most frequent minor species in forests of the Dry Series is the Cordilleran grass *Elymus innovatus,* which in association with *Arctostaphylos uva-ursi, Shepherdia canadensis,* and numerous other species characteristic of semi-open woodland, forms the ground vegetation on appropriate sites under forests of pine, spruce and aspen from western Manitoba to western Alberta.

(2) The Fresh Series of forests, on well-drained soils, includes many shrub and herb types, but moss types are uncommon except on the cooler than normal sites. Dominating trees are aspen, white spruce, jack pine, and paper birch, either in pure stands or in mixture.

Corylus cornuta dominates the fresh, tall shrub types, particularly along the southern edge of the forest section. On the plateaux of the Cretaceous Hills and in the northern districts, *Alnus crispa* becomes prominent as *Corylus* declines. Other tall shrubs—*Prunus virginiana, P. pensylvanica, Amelanchier alnifolia*—characterize some aspen, pine and spruce stands, usually in association with *Corylus.* Medium shrub types in which *Vaccinium myrtilloides* or *Diervilla lonicera* are important occur occasionally.

The absence of shrubs, whether due to a failure of invasion after destructive fires, or to the eliminative action of a closing canopy, may allow herbs to come to the fore. Common species which often contribute to a definite tall herb stratum under pine, poplar, spruce or mixed forests, are *Aralia nudicaulis* and *Chamaenerion spicatum,* with which in turn are associated *Actaea rubra, Aster ciliolatus, Disporum trachycarpum,* and *Viola rugulosa.* Under closer tree canopies, the medium and low herbs are prevalent, with *Oryzopsis asperifolia, Galium septentrionale, Maianthemum canadense* var. *interius,* and *Pyrola* spp. conspicuous in some places.

(3) The Moist Series of forests, on soils of only moderate drainage, includes many communities. All layers of the undergrowth may become prominent in association with various mixtures of all the tree species.

Wherever the stands are such that considerable light penetrates the canopy, tall shrubs often play a primary role in the undergrowth. In the eastern part of the forest section, particularly in the Cretaceous escarpment area, *Acer spicatum* is a characteristic shrub under stands of aspen and aspen-spruce. *Corylus cornuta* continues to be abundant but with it appears *Viburnum trilobum* and occasional *Sorbus decora.* Similarly *Aralia nudicaluis* and *Chamaenerion spicatum* continue to be common in tall herb types, although their association with more mesophytic species such as *Solidago lepida, Mertensia paniculata, Petasites palmatus,* and *Heracleum maximum* is significant of the shift toward the moister side of the gradient.

In coniferous stands, a low herb vegetation is usual, with a high percentage of the cover contributed by *Cornus canadensis, Linnaea borealis* var. *americana, Rubus pubescens, Galium triflorum,* and *Petasites palmatus.* Although such herb types of undergrowth are common in young coniferous stands, the feather moss stratum apparently develops only with age and is rarely present until stands are more than 70 years old. The development of the moss floor (*Calliergonella-Hylocomium*) is accompanied by the appearance of such species as *Goodyera repens, Habenaria orbiculata, H. obtusata, Pyrola virens,* and *Trientalis borealis.*

(4) The Very Moist Series of forests occupies imperfectly drained soils. All tree species enter into the possible cover composition, although jack pine and tamarack are relatively unimportant.

The primary tall shrub under many stands of aspen, balsam poplar, and white spruce is *Cornus stolonifera. Salix* species frequently contribute to the tall shrub stratum, particularly in young stands occupying burned-over areas. Medium shrub types are sometimes seen in which *Viburnum edule, Rubus idaeus,* and *Ribes* spp. are conspicuous, particularly in association with mature and overmature coniferous stands. In some of the more open poplar-spruce or poplar stands, a distinctive tall herb stratum is formed by *Calamagrostis canadensis* plus such additional species as *Anemone canadensis, Aster umbellatus* var. *pubens,* and *Cinna latifolia.* The tall ferns *Pteretis pensylvanica* and *Athyrium filix-femina* var. *Michauxii* are sometimes prominent under forests on very moist alluvium.

In the closer spruce and spruce-fir stands, herb types feature the same species as in the moist series, but *Equisetum* species appear, with *Circaea alpina, Dryopteris* spp. and *Mitella nuda.* A moss stratum forms on the ground early in the life of these stands, and older forests almost invariably show a more or less continuous carpet of *Hylocomium splendens, Calliergonella schreberi, Dicranum rugosum,* and *Hypnum crista-castrensis.*

(5) The Wet Series of forests on soils of poor

drainage and high organic content features stands composed of three tree species: white spruce, black spruce, and the larch, or tamarack. The latter is the species most tolerant of excessive moisture, hence its pioneer role in the forest invasion of fen and peat soils. On firmer and slightly drier peaty deposits, in areas of stagnating ground water, black spruce is the typical tree. White spruce shows a tendency to colonize the fen and muck soils which apparently form under the influence of various conditions such as alkalinity of substratum, grass-sedge vegetation and moving ground water.

The commonest tall shrub type is characterized by *Alnus rugosa,* associated usually with tamarack and white spruce. Tall *Salix* spp. are also common in the Wet Series, but their intolerance tends to reduce their role rapidly as the forest stands develop. The medium shrub types of black spruce are well-known, particularly those in which *Ledum groenlandicum, Chamaedaphne calyculata, Kalmia polifolia,* and *Andromeda polifolia* are prominent. In white spruce forests, *Ribes* spp., *Rubus idaeus,* and *Rhamnus alnifolia* are the common medium shrub associates. Tall herbs are rarely conspicuous in stands of tamarack or black spruce, but the open variants of the swamp border white spruce stands sometimes show a well defined layer in which the tall *Cirsium muticum, Aster puniceus,* and *Sium suave* appear with grasses and sedges. The latter (*Carex* spp.) characterize many stands of spruce and tamarack.

One readily recognized medium herb type of spruce stand has a dominant stratum of *Equisetum arvense* and *E. pratense,* associated with the mosses and low herbs that also appear in the Very Moist Series. Well-defined moss types are common, with *Hylocomium splendens, Climacium americanum, Aulacomnium palustre,* and *Mnium* spp. on the fen and muck soils, and with *Sphagnum* spp. or *Camptothecium nitens* on the deep peats with black spruce.

Groups of Species as Indicators of Moistness of Site

Those who are thoroughly familiar with the vegetation of a particular region are often able to judge the moisture relations of any given community with considerable accuracy. Unfortunately, the approach through experience is not possible for everyone, and a more objective method that all may use is desirable. The vegetation table (Table I) offers some help, for if the moisture-preference groupings are soundly based then it should be possible to use them in interpreting the moisture relations of particular sites. To take an artificial example, a site supporting *Cornus stolonifera, Ribes hirtellum,* and *Dryopteris cristata,* should be similar in moisture conditions to one supporting *Viburnum edule, Mitella nuda,* and *Hylocomium splendens,* as all six species are in the "Very Moist" group. The species composing actual plant communities never fall entirely within one moisture-preference group as in this example, and therefore it is difficult by inspection alone to determine what moisture regime is indicated.

Various methods were tested in an attempt to derive for any given sample of forest vegetation a single numerical index, based on the distribution of the species as checked on the vegetation table. The following practical and theoretical considerations guided the development of a "Vegetation Moisture Index":

(1) For maximum usefulness the method must be simple—not much more than the recognition of the plant species can be expected of those who will use it. Therefore, the index must be derived from presence or absence of species rather than from features such as cover and density which are difficult to assess without careful quadrat or line intersect studies.

(2) Certain accommodating species occupy a wide range of habitats. The broad ecological amplitude of such species (here called "ubiquists") renders them of inferior value as indicators. Little weight should be given to them when calculating a moisture index, even though they may be very prominent constituents of the vegetation. Preliminary studies are necessary to determine which species fall into the category of "ubiquist."

(3) Rare plants—defined as those which in studies of presence are last to be found—should be used very cautiously in working out a moisture index, since the danger is always present that members of this group are ephemeral invaders from outside the community.

(4) The ecological amplitude of species listed in the Very Moist and Wet columns is, in general, narrower than that of species on the fresh and dry side of the gradient. In other words, the former are better indicators than the latter and should be given more weight when an index is being worked out. Why this should be so is not clear, but it is apparent in the field that the more mesophytic and hydrophytic species are tied rather closely to their appropriate habitats, while plants which are able to tolerate drier conditions are not by that fact necessarily confined to the drier sites.

The method which was adopted as giving the most satisfactory results assigns weights of 1, 2, 4, 8, and 16 to species which occur in the Dry, Fresh, Moist, Very Moist, and Wet columns, respectively. The geometric increase of the values is a recognition of the greater significance of species on the wetter side of the table. Ubiquists are omitted from the calculations, as also are rare species except in particular circumstances. Steps in the calculations are as follows:

(1) A special field sheet, drawn up in the same form as the vegetation table (Table I) and listing the important forest species of the district in their appropriate moisture-preference columns, is used. Ubiquists, identified from preliminary studies, are specially marked, so that they can be easily separated from the others in subsequent calculations. A place is provided for noting the dominant and secondary strata of the undergrowth ("tall shrub," etc.) which characterize each stand.

(2) The investigator checks off all the species which he finds in the particular stand being studied. In practice, it has been found preferable to enter beside each species an ocular estimate of cover-abundance, as this increases the value of the list for other phytosociological purposes. The scale used, slightly modified from Braun-Blanquet, is given below:

5—covering 76 to 100 per cent of the ground
4—covering 51 to 75 per cent
3—covering 26 to 50 per cent
+2—covering 16 to 25 per cent
2—covering 6 to 15 per cent
+1—covering 3 to 5 per cent
1—covering 1 to 2 per cent
+—covering less than 1 per cent (rare).

By specifying in the field instructions that on each plot a minimum number of species (usually 25) must be listed in addition to the ubiquists, an adequate sample is assured.

(3) On completion of the tally, the species in each of the five moisture columns are summed, and the totals are weighed by multiplying by the appropriate number, whether 1, 2, 4, 8, or 16. At this stage, the ubiquists are excluded, and the rare species are used only when their omission would reduce the sample below 20 species or so.

(4) The figures from all columns are now summed, the total is divided by the number of species entering into the previous calculations, and the quotient is multplied by 10 to eliminate the decimal. The resulting figure is the Vegetation Moisture Index, abbreviated hereafter as the VMI.

The VMI was worked out for various forest sample areas in Manitoba and Saskatchewan during the field season of 1954, and it was found that stands in which white spruce is a constitutent species segregated along an index gradient from 20 (driest) to 80 (wettest). Three examples are shown in Table II.

If there were some objective method of determining the soil moisture regimes of given homogeneous areas, then it would be possible to check the reliability of the VMI's, but none such exists. The system proposed by Hills (1950, 1952) is one of the least subjective which may be used, because it derives moisture regimes of sites primarily from the study of soil profile development, pore pattern of parent material, and topographic position—all determinable with a fair degree of exactitude. Briefly, within a given climatic region a standard moisture regime (defined as providing optimal moisture conditions, without excess, for the best development of mesophytic vegetation) is identified, and all sites are judged relative to this standard regime, using an 11-point scale which ranges between the extremes of arid (symbol Θ) and saturated (symbol 9). Basic work along these lines was carried out in conjunction with quadrat studies of minor vegetation on one-tenth-acre forest sample plots at the Riding Mountain Forest Experimental Area in 1952, hence a comparison was possible of soil moisture regimes according to Hills' methods, and of VMI's as worked up from the quadrat frequency-abundance data. Table III shows the results from Plots 301 to 316, inclusive, the VMI's being worked up from the 25 most frequent species, exclusive of ubiquists, on each plot.

A good correspondence between increasing moisture regime and increasing vegetation moisture index is shown. There are a number of reasons why the two scales do not coincide. The soils moisture regimes were determined from the examination of single soil pits, in other words, they represent "point" studies, while each VMI was derived from the areal study of an entire plot. For this reason, the best correspondence is to be expected on very homogeneous plots, and the poorest on those of irregular surface or on slopes, as the notes in the table suggest. Also, of course, the use of plants as indicators is not straightforward. A complicating factor stems from differences in rooting habits of each species, for small plants are influenced primarily by soil surface conditions while large species are influenced by the deeper as well as the shallow soil horizons. Thus, the small herbs on strongly leached, surface-dry soils may reflect more xeric conditions than do the associated tall shrubs and herbs, but on the same sites the comparative moisture indications of the small and large plants may be reversed if much moist decayed wood lies on

TABLE II. Vegetation of a Dry, a Moist, and a Wet forest stand, showing the derivation of Vegetation Moisture Indices

A. Plot 500 - Duck Mountain Forest Reserve, Manitoba.
Open white spruce and aspen stand on excessively drained till.
Dry, grass-herb community (*Elymus-Fragaria-Arctostaphylos*).

"Very Dry and Dry": 14 species (plus 3 rare)
4 Elymus innovatus
2 Arctostaphylos uva-ursi
1 Agastache foeniculum
1 Hedysarum alpinum var. americanum
1 Potentilla arguta
1 Astragalus alpinus
1 Halenia deflexa
1 Anemone multifida
1 Aster laevis
1 Comandra richardsiana
1 Oryzopsis asperifolia
1 Polygala senega
1 Oxytropis gracilis
1 Viola adunca
+ Lilium umbellatum
+ Solidago hispida
+ Antennaria campestris
"Fresh": 5 species
1 Amelanchier alnifolia
1 Lathyrus ochroleucus
1 Thalictrum venulosum
1 Vicia americana
1 Viola rugulosa
"Very Moist": 1 species
1 Salix bebbiana
"Ubiquists": 6 species
3 Fragaria virginiana
1 Rosa acicularis
1 Aster ciliolatus
1 Galium septentrionale
1 Schizachne purpurascens
1 Smilacina stellata
Sum of the weighted values of the species in each moisture group:
(14 x 1)+(5 x 2)+(1 x 8)=32
VMI: 32/(14+5+1)=1.6 x 10=**16**

B. Plot 512 - Duck Mountain Forest Reserve.
Mature white spruce and birch, on moderately drained till.
Moist, tall shrub-and-herb community (*Corylus-Aralia-Mitella*).

"Dry": 1 species (plus 1 rare)
1 Oryzopsis asperifolia
+ Elymus innovatus
"Fresh": 3 species (plus 4 rare)
3 Corylus cornuta
1 Symphoricarpos albus
1 Lathyrus ochroleucus
+ Prunus virginiana
+ Actaea rubra
+ Chamaenerion spicatum
+ Pyrola secunda
"Moist": 7 species
2 Mertensia paniculata
2 Petasites palmatus
2 Cornus candaensis
2 Rubus pubescens
1 Pyrola virens
1 Viola renifolia
1 Linnaea borealis var. americana
"Very Moist": 8 species (plus 1 rare)
2 Viburnum edule
2 Circaea alpina
2 Mitella nuda
1 Cornus stolonifera
1 Ribes hirtellum
1 Ribes triste
1 Rubus idaeus
1 Galium triflorum
+ Dryopteris cristata
"Ubiquists": 6 species (plus 1 rare)
3 Aralia nudicaulis
1 Rosa acicularis
1 Aster ciliolatus
1 Galium septentrionale
1 Fragaria virginiana
1 Maianthemum canadense var. interius.
+ Schizachne purpurascens
Sum of the weighted values of species in each moisture group:
(1 x 1)+(3 x 2)+(7 x 4)+(8 x 8)=99
VMI: 99/(1+3+7+8)=5.2 x 10=**52**

C. Plot 510 - Duck Mountain Forest Reserve.
Mature white spruce, on poorly drained (muck) soil.
Wet, herb-moss type (*Equisetum-Mnium*).

"Fresh": 1 species (plus 1 rare)
1 Disporum trachycarpum
+ Chamaenerion spicatum
"Moist": 3 species
2 Mertensia paniculata
2 Cornus canadensis
1 Petasites palmatus
"Very Moist": 11 species (plus 2 rare)
5 Mnium spp.
3 Mitella nuda
1 Viburnum edule
1 Ribes hirtellum
1 Ribes triste
1 Anemone canadensis
1 Heracleum maximum
1 Circaea alpina
1 Galium triflorum
1 Habenaria obtusata
1 Moneses uniflora
+ Ribes glandulosum
+ Poa palustris
"Wet": 2 species (plus 2 rare)
5 Equisetum arvense
1 Carex disperma
+ Ribes hudsonianum
+ Stachys palustris
"Ubiquists": 4 species
1 Aralia nudicaulis
1 Aster ciliolatus
1 Schizachne purpurascens
1 Fragaria virginiana
Sum of the weighted values of species in each moisture group:
(1 x 2)+(3 x 4)+(11 x 8)+(2 x 16)=134
VMI: 134/(1+3+11+2)=7.9 x 10=**79**

the ground. In general, however, there is a good correspondence between moistness of site and the associated elements of the vegetation, although the calculation and interpretation of the VMI requires the use of common sense in particular situations.

Two additional facts support the contention that the proposed method of determining a moisture index for sites, using the groupings of species shown in the vegetation table, will be found useful in the field. The first is that communities on long slopes segregate out as expected, with a relatively low VMI on the upper slope and a relatively high VMI on the lower slope. As an example, the following VMI's were calculated on five plots sampling the forest on a north-facing hillside in the Duck Mountain Forest Reserve, Manitoba—36, 43, 42, 44, 48—this representing the sequence from a birch stand on the upper slope to a spruce stand on the lower slope.

TABLE III. Comparsion of soil moisture regimes and vegetation moisture indices on sixteen one-tenth-acre plots

Plot number	Soil moisture regime	Vegetation moisture index	Remarks
301	0	22	
308	1	18	
303	1	23	
316	1	23	
306	1	24	
313	2	28	
304	2	30	Slope community
307	2-3	28	
312	3	29	
305	3	32	
310	4	41	Uneven surface
309	4-5	39	
311	5	46	
302	5	49	
314	5	64	Depression in plot
315	6	65	

The second supporting fact is that samples of different vegetation growing on apparently similar sites work up to similar VMI's. For example, it it common to find patchy forest types in which well-stocked areas with a shade-type flora alternate with small, more open areas where better light conditions allow the development of a richer community. Provided that the patches are not so large as to cause marked differences in such factors as root distribution of the trees, surface temperatures and moisture, then it has been found that the VMI's of the closed and open patches usually fall very close to one another.

It is not claimed that the VMI provides more than a rough measure of site conditions, yet it apparently has possibilities which could be improved by more exact knowledge of the comparative responses to moisture of the forest species. Used in conjunction with Hills' physiographic sites (*op. cit.*) it may prove to have considerable value, since it can be called upon where soil conditions are difficult to interpret or where the emphasis is on rapid reconnaissance. For a given district, it would seem feasible to correlate soil moisture regimes and VMI's so that both might be used together or interchangeably. In Table IV an equivalency is tentatively suggested for the Riding Mountain and Duck Mountain areas at the southeastern extremity of the southern boreal forest in Manitoba.

TABLE IV. Equivalence of VMI classes and soil moisture regimes in forests of the Riding Mountain and Duck Mountain areas, Manitoba

VMI classes (Rowe)	Moisture regimes (Hills)	General moisture class
Less than 25	0, 1	Very dry and dry
25-28	2	Moderately fresh
29-34	3	Fresh
35-42	4	Moderately moist
43-52	5	Moist
53-65	6	Very moist
More than 65	7, 8	Wet

As a comment on Table IV, it might be supposed that all "dry" plots should place in the 10 to 20 VMI range and that all "wet" plots should place in the 80 to 160 VMI range. However, in almost every kind of forest community there has been found a scattering of species from the Fresh and Moist groupings whose presence tends to raise the VMI of the dry plots and lower the VMI of the wet ones. Therefore the data in hand suggested that all VMI's less than 25 should be designated "dry" and all greater than 65 "wet." The intermediate classes have been made of unequal width, increasing by 4, 6, 8, 10, and 13 units from dry to wet, in recognition of the theoretical tendency toward a geometrical increase in VMI that follows from the geometrical increase in weight of each succeeding moisture class.

The vegetation table, the vegetation moisture index, and the VMI classes in Table IV have all been drawn up with a view to their usability in one particular forest district where the majority of stands are dominated by white spruce and aspen. Studies in other districts, or studies emphasizing other cover types, would require that new tables be devised to take account of the significant species. For example, work confined to jack pine types would require a considerable expansion of the left-hand side of the table, as species in the two right-hand columns (Very Moist, and Wet) would be omitted. The same approach could nevertheless be used.

DISCUSSION

Various classifications of forest types and forest sites have been built around the concept of gradients in environmental factors, as the following examples illustrate. Heimburger (1934) has summarized some of the early European work on forest typology, and among others he refers to Pogrebnjak who "plotted the natural limits of distribution of certain plants on two axes representing the main edaphic factors of growth, namely, mineral soil fertility and moisture." Thus, a series from poor-to-rich nutrient status was combined with a series from dry-to-wet moisture regime, and the scheme was applied to yield classes for forest trees. A similar approach to the classification of forest communities in Russia can be seen in the work of Sukachev (1928).

More recently, Anderson (1950) classified "locality units" on a coordinate system, using six fertility and four moisture groups. The resulting site classes were named after the predominant plant species usually occurring on them. Tore Årnborg (1950) has used a similar system in a forest site classification for northern Sweden, with five moisture classes (arid, dry, fresh, moist, wet) and four nutrient-regime classes which, from poorest to best, are indicated by dominance of the following: ericaceous shrubs, oak fern with ericaceous shrubs, herbs with ericaceous shrubs, and herbs. In addition to these examples drawn from forestry literature, many more references could be quoted to illustrate the considerable interest that is presently being shown by ecologists in "gradient analysis" as an approach to specific problems of vegetation. (See, for example, Whittaker 1954.)

It cannot be expected that the distribution and growth of plants will always show a nice correlation with gradients in the intensity of particular factors, as compensatory influences in the environment plus variable ecological tolerances in the plants will tend to conceal much of these relationships. Nevertheless, detectable responses of plants to factor variations do occur, and careful study by appropriate techniques will disclose them.

The responses of plants to variations in intensity of light and of moisture have been discussed at length in the main body of this article. Two other environmental factors, or rather factor-complexes, whose gradients might profitably be correlated with plant indicators are soil fertility and ecoclimate. Mention has just been made of fertility series set up by some investigators for purposes of site classification. Much of the reported work is highly subjective, however, partly because the concept of fertility is poorly defined and partly because of a lack of knowledge of the optimal nutrient requirements for trees and the plants that grow with them. An improved approach to the problem must include studies of the soil, as is illustrated for example in recent work by Wilde and Leaf (1955).

The other factor-complex, ecoclimate, has been little studied in relation to plant indicators. One fruitful line of research is the study of plant distributions, as the range of a species suggests the climatic conditions to which it is adapted. Thus, within the boreal forest the warmer sites are often characterized by plant migrants from the eastern deciduous forest, while colder sites are frequently inhabited by arctic-alpine plants. A second approach can be made through studies of phenology, for the periodicity of leafing, flowering, and fruiting is closely related to climatic influences.

The suggestion is made here that the methods used in the development of a Vegetation Moisture Index might also be applied in working out indices of other important factors or factor-complexes. The approach is as follows: First determine, as exactly as possible, the relative positions of the plant species along a gradient from low intensity to high intensity of the selected environmental factor. As has been pointed out, this requires intensive field work, combining close observation and good judgment with whatever instrumental measurements and analyses are appropriate. Next, divide the gradient into classes or series, and assign empirical weights to each. When calculating the final index from given samples of vegetation, take into account only the species whose significance in respect to the factor concerned is reasonably assured.

Summary

1. No system of describing stands in general terms has hitherto been available for the southern boreal forest of Manitoba and Saskatchewan. A simple scheme based on the physiognomy of the undergrowth and on moistness of site is outlined.

2. As an aid to stand description, a vegetation table is presented, showing the positions of about 200 common forest species relative to one another so far as their heights and their moisture preferences are concerned. For field use, a sheet has been drawn up in the form of this table, and the species occurring in plots or stands under study are checked off on it. The resulting scatter pattern provides a basis for the interpretation of site moistness, successional status of the community, density of canopy, and so forth.

3. Some of the commoner forest communities in the southern boreal forest of Manitoba-Saskatchewan are briefly described using the moisture-physiognomy scheme, and mention is made of some of the prominent species.

4. The possibility of using the groupings of species in the five moisture series, as shown in the vegetation table, for the interpretation of moistness of site is examined, and a method of working out a Vegetation Moisture Index is proposed. This index is compared with moisture estimates derived from the study of soils and topography, and a good correspondence is shown.

5. It is finally suggested that the method used in working out an index of moistness from the plant species present on a particular site could also be used to derive indices of soil fertility and ecoclimate for use in stand description and in forestry research.

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PERCENTAGE LIGHT READINGS, THEIR INTENSITY-DURATION ASPECTS, AND THEIR SIGNIFICANCE IN ESTIMATING PHOTOSYNTHESIS[1]

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Frequently ecologists describe the light conditions found in ecological situations in terms of the percentage of possible full sunlight they receive. These percentages, usually derived from light readings made on a clear day around noontime, are used to characterize the light conditions of a habitat and are often used to help explain the photosynthetic responses of species in that habitat or experimental area.

Although per cent full light classifies light conditions in a general way, its meaning in terms of photosynthesis and plant growth is difficult to determine. This is because plants do not react photochemically with percentages of full light, but rather with particular intensities over specific periods of time.

To obtain some concept of the quantitative meaning of per cent full light measurements, the intensity-duration aspects of light were determined, from May 3 to October 26, 1954, for unshaded plots, 100% f.l., and for plots artificially screened to permit transmission of 58% f.l. and 29% f.l., respectively (Fig. 1). These data, presented here, give useful information on intensity-duration relationships of light during the growing season and on the quantitative effects of shading on seasonal light distribution. They also permit an evaluation of certain speculations on important plant-light interactions formerly based on per cent f.l. readings alone.

METHODS

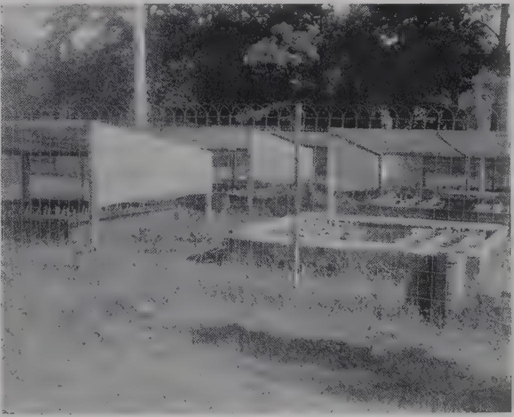

FIG. 1. Plots on the Emory University Campus: right foreground, an unshaded plot; left foreground, a plot shaded to 29% full light; center, two plots shaded to 58% full light. The open end of the shades faces north.

The shaded plots, screened on top and to within one foot of the ground on the east, south, and west sides, permitted a certain amount of sky radiation to enter unscreened from the north (Fig. 1). Consequently a somewhat higher percentage of light occurred under the screens during times when the relative amount of sky radiation was high, for example, on hazy days. However, light measurements made under the screens on cloudy, hazy, and overcast days indicated that the increase in percentage of light was relatively small, averaging about 1 to 3 per cent, and that the screening effect was more or less constant for all sky conditions.

In the absence of a continuous recorder, a generalized picture of light conditions during the experimental period was calculated by establishing a relationship between light readings taken over the plots located on the Emory University Campus and the continuous light record made on an Eppley pyrheliometer at the Atlanta Airport 11 miles away. Assuming that the insolation received at these two locations were essentially the same, the relationship permitted the conversion of pyrheliometric readings to foot candles of visible light over the plots.

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[1] This work was done with the aid of National Science Foundation Grant, G909, while the author was a member of the staff of the Biology Department, Emory University.

On uniformly bright or overcast days between July 27 and August 7, 1954, light readings in foot-candles were taken over the plots, hourly, from dawn to dusk with a recently calibrated Model II Weston Illuminometer. For each set of three plot-light readings, a corresponding pyrheliometric reading in langleys (gram cal/cm^2/min.) was obtained. Regression equations of the form $Y = a + bx$ were then calculated for each plot-light condition where Y = light intensity in foot-candles, a = a constant, b = the regression coefficient, and x = the phyreheliometric reading in langleys. The calculated regression curves are shown in Figure 2.

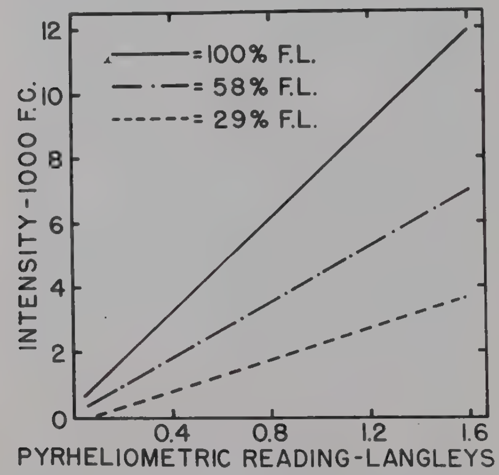

FIG. 2. Regression curves showing the relationship between light intensity, in foot-candles, occuring over the various plots on the Emory University Campus and the pyrheliometric readings made at the Atlanta Airport.

Following the construction of the curves, the continuous record was interpreted in terms of light conditions existing over the plots. A negative microfilm record[2] of the pyrheliometric charts from May 3 to October 26, 1954, exclusive of 18 hours in July when the recorder was not in operation, was examined, and the reading for each of the 2315 hours of light was visually averaged and recorded in langleys. The number of hours in each langley class was then summed and the langleys were converted to foot-candles in accordance with the curves shown in Figure 2. The hours of light received were then tabulated by 500 foot-candle classes for each plot-light condition (Table I). This record roughly corresponds to the light received during the growing season.

Separate regressions, not shown here, were calculated for the first two hours after sunrise when the plots were shaded by a nearby building. Data for these hours were treated as above and incorporated into Table I.

TABLE I. Estimated distribution of light intensity in 500 foot-candles classes over plots with various conditions of shading. May 3 to October 26, 1954

	NUMBER OF HOURS			PERCENTAGE DISTRIBUTION		
Intensity in f.c.	100% full light	58% full light	29% full light	100% full light	58% full light	29% full light
0-500	194	416	655	8.4	17.9	28.2
501-1000	227	191	265	9.8	8.2	11.4
1001-1500	139	155	249	6.0	6.7	10.7
1501-2000	69	137	302	3.0	5.9	13.0
2001-2500	78	139	351	3.4	6.0	15.1
2501-3000	102	131	314	4.4	5.6	13.5
3001-3500	59	180	171	2.5	7.8	7.4
3501-4000	106	122	8	4.6	5.3	0.3
4001-4500	64	162	...	2.8	7.0	...
4501-5000	93	213	...	4.0	9.2	...
5001-5500	73	171	...	3.1	7.4	...
5501-6000	82	163	...	3.5	7.0	...
6001-6500	109	109	...	4.7	4.7	...
6501-7000	76	26	...	3.3	1.1	...
7001-7500	90	...	...	3.9	...	...
7501-8000	113	...	...	4.9	...	...
8001-8500	148	...	...	6.4	...	...
8501-9000	67	...	...	2.9	..	...
9001-9500	128	...	...	5.5	...	. .
9501-10000	97	...	...	4.2	...	...
10001-10500	104	...	...	4.5	...	...
10501-11000	44	...	...	1.9	...	..
11001-11500	34	...	...	1.5	...	...
11501-12000	19	...	...	0.8	...	...
Totals	2315	2315	2315	100	100	100

RESULTS

The majority of the 2315 hours of light falling on the unshaded plots, 100% f.l., was not received at the higher intensity levels, but was more or less evenly distributed over the whole range of intensity from 0 to 12,000 f.c. (Table I). Only 44.5% of the hours was above 6000 f.c., the mid-point intensity, while 55.5% was below it. The comparatively fewer hours of light at the higher intensities resulted from the relatively low intensities in the hours just after sunrise and before sunset and from the fact that overcast or cloudy days had intensities far below those on clear days.

As in the instance of 100% f.l., lower per cent f.l. readings, translated into foot-candles, did not typify, even closely, the most commonly found range of intensity under the screens. Equating full light to 10,000 to 12,000 f.c., it might be expected that a large number of hours of light under 58% f.l. would be in the 6000 to 7000 f.c. class, yet only 5.8% of the total hours were found there. Correspondingly, on plots shaded to 29% f.l. only 7.7% of the total light was found in the 3000 to 4000 f.c. class (Table I).

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[2] Obtained through the courtesy of the National Weather Records Center, Asheville, North Carolina.

The principal effects of shading were to reduce the range of light intensities received and to increase the proportion of light accumulated in lower intensity classes (Table I). Considering 0 to 7000 f.c. and 0 to 4000 f.c. to be the range of intensity under 58% f.l. and 29% f.l., respectively, only 41.9% of the total light, in the former, was above the mid-point intensity of 3500 f.c., while in the latter only 36.3% was above the mid-point intensity 2000 f.c.

PHOTOSYNTHETIC SIGNIFICANCE

Assuming that these data for unscreened and artificially screened plots apply to natural situations, at least to unshaded areas and to those in which the degree of shading is more or less constant, certain assumptions on plant-light interaction formerly based on per cent full light readings may be reconsidered.

On the basis of field and experimental studies, it is frequently stated that a certain percentage of full light intensity represents the minimum light requirement at which a species can grow and survive (Burns 1923, Shirley 1945, etc.). This percentage in terms of intensity does not represent the minimum light level at which adequate photosynthesis will occur. Such a small proportion of the total light is received at this intensity, it seems likely that to survive competitively the species must be able to use effectively some of the much larger quantities of light received at lower intensities. Thus, in actuality, the presence of a species in a place shaded to some per cent full light probably indicates an ability of that species to utilize effectively light intensities lower than those represented by the per cent full light reading.

Knowledge of inensity-duration aspects of light permits speculations about growth not advisable on the basis of per cent full light readings alone. This is particularly so in the event that the photosynthetic response of a species is known in its broader aspects.

Species that reach maximum rates of apparent photosynthesis at relatively low light intensities and maintain them up to full sunlight intensity such as white oak, dogwood, eastern red oak (Kramer and Decker 1944), red maple, yellow poplar, overcup oak (Kozlowski 1949), sweetgum (Bormann 1953), might be expected to make about equal growth in shaded, low per cent full light, and unshaded, 100 per cent full light, areas. However, all other things being equal, this seems unlikely: firstly, because all light intensities above the minimum intensity at which maximum photosynthesis will occur will evoke the same amount of apparent photosynthesis per unit of light received; and, secondly, because unshaded areas receive many more hours of light above the minimum intensity needed to evoke maximum photosynthesis. For example, the above listed species attain their maximum rates of apparent photosynthesis at approximately 2000 f.c. If they had grown on the unshaded plot, 100% f.l., they would have received 1686 hours above the minimum intensity, while if they had grown on the plot shaded to 29% f.l. they would have received only 844 hours above the 2000 f.c. minimum intensity (Fig. 3).

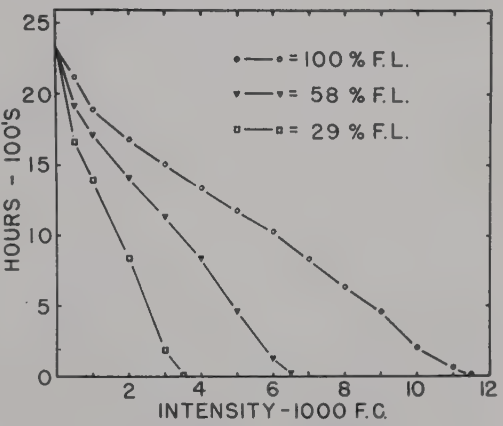

FIG. 3. The effect of screening on the number of hours of light received above various intensities.

As a result of these considerations, species like those mentioned above would be expected to achieve their greatest growth in unshaded areas. Approximately equal amounts of growth under sunny and shaded conditions, such as reported by Kozlowski (1949) for overcup oak, probably indicates that the species is unable to utilize higher light intensities as effectively as lower ones or that other factors, such as temperature and soil moisture, may nullify the light effects.

SUMMARY AND CONCLUSIONS

1. The intensity-duration aspects of light received under various degrees of artificial shading were estimated for the period from May 3 to October 26, 1954.

2. Intensity-duration aspects of light received under three degrees of shading, 100% full light, 58% full light, and 29% full light, were analyzed and the following points were made:

a. The per cent full light reading, in terms of intensity, did not typify even closely the most commonly received intensities.

b. The majority of light received on shaded or unshaded plots was below the middle point of the range of intensity of that plot.

c. The principal effects of shading were to reduce the range of light intensity received and to increase the proportion of light accumulated in lower intensity classes.

3. Certain assumptions on plant-light interaction based on per cent full light measurements are reconsidered, and it is suggested that per cent full light readings do not make a substantial basis for the explanation of photosynthetic reactions of species.

a. Per cent full light readings can have a limited usefulness in explaining photosynthetic reactions if items 2a, 2b, and 2c are taken into consideration.

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POLLEN PROFILES AS INDICATORS IN THE HISTORY OF LAKE FILLING AND BOG FORMATION

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INTRODUCTION

From a small beginning—when the Swedish ecologist von Post conceived the idea that microfossils (pollen in this case) could be used as indicators of forest changes and indirectly also as indictors of climatic changes and the retreats and advances of continental glaciers—pollen studies (now dressed in the more impressive term palynology) have received more and more recognition by ecoloigsts, geologists, and radiocarbon dating experts. Interpretations of pollen profiles are, or of necessity should be, based on ecological principles. In modified form they now find valuable use in the spore analysis of coal beds and oil shales. Very little change has been made in the instruments for sampling bogs, but sampling equipment for lake sediments has seen more significant developments. In my estimation, the Swedish Hiller borer (or modifications of it) is still the most satisfactory instrument in the field of bog boring. With it one can take samples in comparatively soft sediments—also it is more under control of the operator than the Davis borer, and so leaves less possibility for error to enter the picture. I was delighted with what I saw of Dr. J. R. Vallentyne's work in Lake Opinicon, Ontario, using his modification of the Livingstone sampler. The Courtemanche permafrost borer, on which I reported in the January, 1955, issue of ECOLOGY, is in my estimation a fine companion instrument to the Hiller outfit in regions where permafrost presents special problems.

During the years, methods have been examined for defects and were criticised or approved, or left with a shrug of the shoulder if no solution could be found, as for instance in the annoying problem of over- and under-representation of certain genera in the pollen rain. In the United States, for some reason, we have not taken lake dynamics sufficiently into consideration, and we apparently have not, to the fullest extent, realized that the bogs of today are the "mummies" of former dynamic water bodies. So lakes south of Lat. 58, Quebec, are operating under different sedimentation dynamics today than they did in their early youth. Young lakes which I have observed in the tundra of Ungava show no evidence of centripetal filling even though they have been collecting organic material for 2000 years or longer. See Figure 1.

A quarter century ago and before, we followed the desk philosophy stimulated by peripheral sur-

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[1] Excerpts from the address delivered as retiring President of the Ecological Society of America at the A.I.B.S. meeting at East Lansing, Michigan, September, 1955.

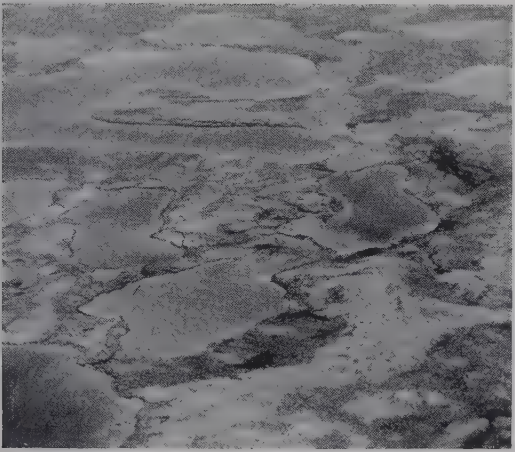

FIG. 1. Aerial photograph of young lakes east of Port Harrison, Ungava. 60°29′N, 77°56′W.

face observation in the field. The so common open central pools of bogs almost in the "verlandet" stage, were considered mute evidence that filling proceeded centripetally until the lake was obliterated. According to such a theory, it would make no difference where in a bog a boring was made in order to obtain the record from the very genesis of accumulation and the very earliest vegetational history. This was the concept which I took into my early bog boring expeditions, and it was truncated pollen profiles which brought the realization that lakes, initially at least, do not fill centripetally—and made me very cautious of the location where a boring would be made. In northern Indiana, we have five, easily recognized, major vegetational changes—1, spruce; 2, pine; 3, pine-oak; 4, oak; 5, oak and various other broad-leaved genera (*Fagus, Acer, Juglans, Ulmus,* etc.) Absence of the spruce period in Indiana bogs, especially when borings were made at the border of small central pools, suggested the thought that lakes initially did *not* fill in as assumed, centripetally, and even in completely filled-in bogs we initiated the custom of making soundings to locate the deepest part of the basin, and of always making our borings in this area. Since that time, I have always carried a microscope into the field station to check all bottom samples—at least, I have checked on possible unusual basin characteristics which might result in truncated profiles.

I am not a limnologist, but I gave much thought to the dynamics of lakes along the shearing plane, and the thought occurred to me that water movement was no doubt retarded in the deeper parts of lakes, thus reducing carrying power of the currents and causing the settling out of materials in transport. Of course, since then, I have learned that a thermocline is not necessary in order to have the earliest sediments limited to the deepest part of a basin—even shallow lakes show this characteristic. At that time, I was privileged to collaborate with my good friend, Ira T. Wilson, who invented an excellent sampler for boring in deep lakes (Sandusky Bay). I was especially interested in his line transect borings of Winona (Fig. 3), Spear and Shoe Lakes in Indiana, and Douglas, Third Sister, and Fish (Fig. 2) Lakes in Michigan. Tippecanoe and Winona Lakes have a very irregular bottom configuration and thus gave promise of checking whether settling out was determined by the center of a lake, *per se,* or if every deeper part of the basin behaved like the center of a simple basin. Since Indiana forest history is marked by five great forest changes, it seemed logical that a definitely known, complete profile could be used as a master profile against which other profiles (especially such as appear to be incomplete) could be checked.

In spite of the progress which has been made in the study of dynamics of lakes, the extent to which early sedimentation limits the area of a lake basin where palynologists may obtain a core with complete forest history (Fig. 4A) is still inadequately recognized by some workers. Also smaller lakes without a thermocline have not received the attention that has been given to larger and deeper lakes.

We are entering an era of great activity in pollen analysis and lake studies. We are also riding on a tidal wave of new textbooks in general botany, at times with illustrations based on ancient philosophies, and if we are teachers, the old Turkish proverb "It is dangerous to descend into a well on a rotten rope" deserves our earnest consideration. So it seems we are justified in presenting the summary of a quarter century of experience with the "artistic temperaments" of some 185 bog and lake basins and their relationship to pollen analysis.

EARLY EUROPEAN LITERATURE

In the pre-war period, much greater progress in this phase of lake and bog study was made in Europe than in America. In 1901, Forel held the concept that in basins with less than 40° slope, the whole profundal area is uniformly covered with lymnic sediments. By 1928, Lenz described the influence of counter currents to the surface currents produced by waves which transport downward and lakeward where they are halted at the thermocline. To quote Lenz: "As a whole, the amount of sediment increases with depth of basin. In general, we might assume that the effect of

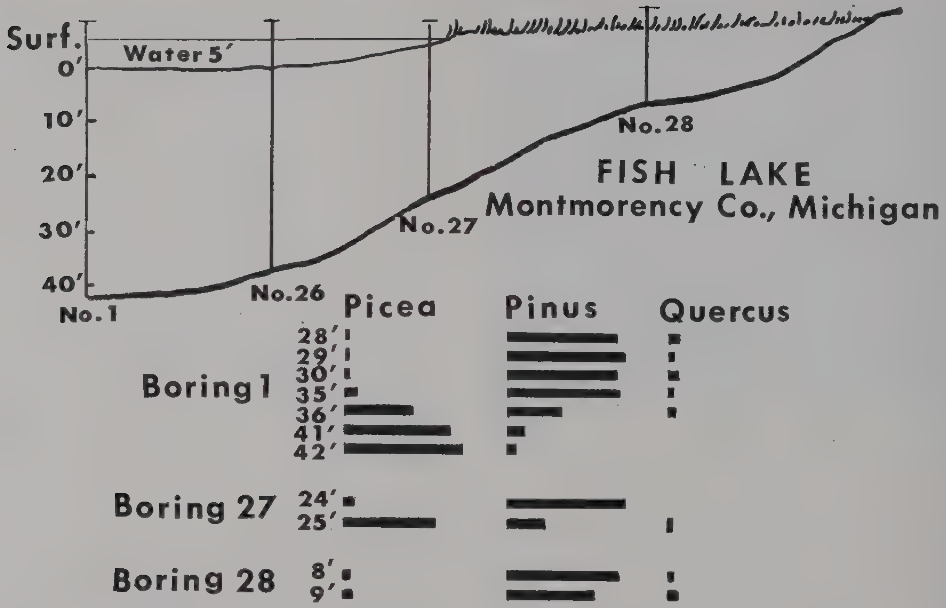
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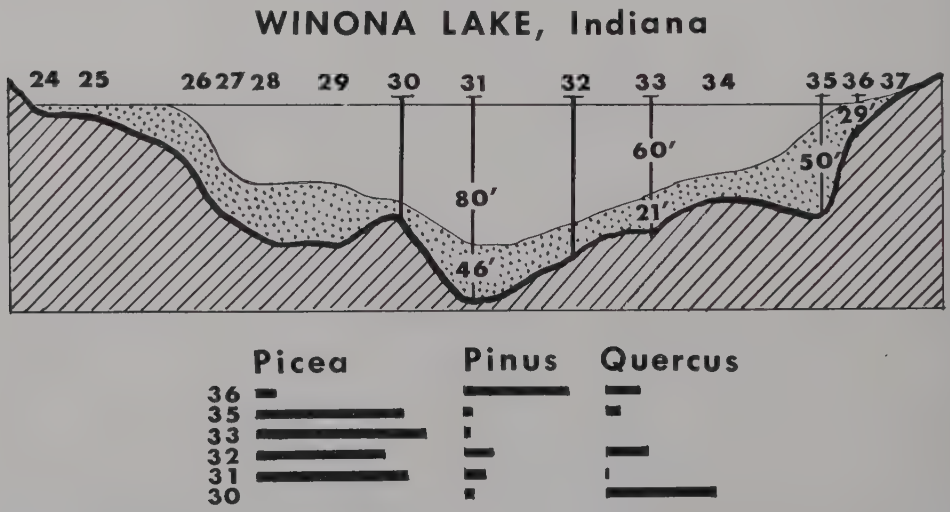
FIG. 2. Fish Lake, Michigan. Diagram of line transect borings in a simple type basin, with resulting pollen profiles showing degrees of truncation.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46'
Picea
Pinus
Quercus
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FIG. 3. Winona Lake, Indiana. Irregular basin with several depressions. Diagram of line transect borings with resulting pollen profiles.

water currents is gradually reduced with depth. Lymnic sediment is distributed with aid of counter currents over the entire profundal part of the basin, fills the deeper depressions and thus produces a uniform level over the whole bottom." He then described the effect of wave action on the windward and leeward side of lakes, saying that on the leeward side, strong counter currents transport organic matter into the deeper part of the basin. This was my own observation in the small Weber Lake in Wisconsin (Potzger and Van Engel 1943). The windward side was in the waterlily and potamogeton stage, while the leeward side was a bare sandy shore to a depth

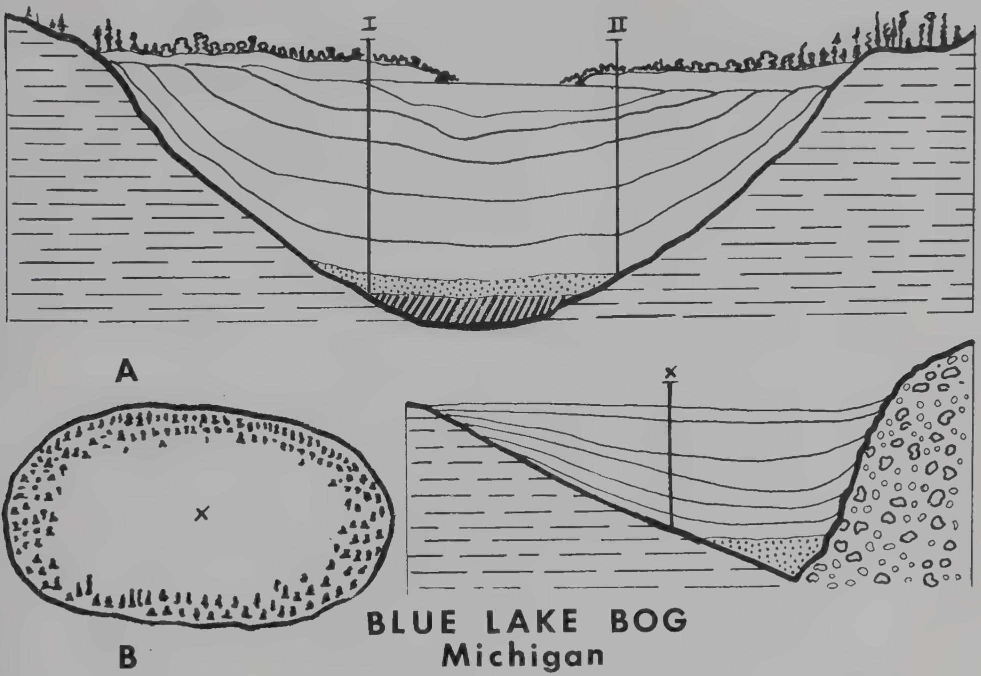

Fig. 4. A.—The author's concept of lake filling in general. Vertical lines mark the often narrow limits, typically near the center, within which sampling will include the earliest sediments. B.—Blue Lake near Muskegon, Michigan. Diagram to show variation from the generalized concept, associated with asymmetrical basin.

of about 4 or 5 feet. Lenz stated that the pollen analysis method of determining history of a lake was excellent. He said "In this manner one is able to make age determinations for the various layers of sediment." In my opinion, not so much time estimates as comparison with forest chronology can be made. Naumann (1921) credited Lundquist (1923-1926) with being the first to use pollen profiles for such diagnostic work. Thienemann (1921) divided lake development into four phases, viz. youth, maturity, old age, and pond or "Weiher" stage. Lundquist said that line profiles were the only solution to the study of dynamics and the order of lake filling. While the work of men like Forel, Gams, Thienemann, Naumann, Lundquist, Lenz, and others had established very well the process by which lakes fill, especially the initial stage, perhaps on the assumption of a uniform simple basin, this seems to have received very little consideration in the United States, and the Thienemann "Weiher" stage is still paraded in publications and textbooks as the *modus operandi* in the youth stage—the centripetal filling process.

In perusal of the European prewar literature, I failed to find adequate recognition and treatment of small kettle bogs, the off-center deepest part of a basin, the complex lake basins, and the relationship of "Weiher" stage to youth stage. Both these stages are very significant for the information of the pollen analyst who aims to get profiles with complete forest history. I am thinking here of the very narrow limits of deposition of initial sediments in deep kettle lakes, at times only 25 to 500 feet, for it is here that the young palynologist makes his mistakes.

The Concept of Centripetal Filling in America

Genesis of the centripetal progress of lake filling to bog formation can no doubt be credited to N. S. Shaler (1890) who wrote, "In such limited water basins the waves produced by wind have relatively little power. The growing pond lilies and rushes protect by their leaves and stems the shores next the shallow bottom from the impact of the waves. Thus sheltered the sphagnum grows space and by the continued supply which it gives to the bottom, still further diminishes the depth of water next the shores which it occupies. As the sphagnum grows from its first lodgment on the shore outwardly toward the center of the lake, the mat it forms floats upon the water and constantly contributes the waste of its dead stems to the peaty accumulation which takes place upon the bottom of the basin. In this way, providing the pool be not originally deep, it requires but a few thousand years to close over the surface and reduce the original expanse of the water to the condition of a quaking bog." In his Figure 16, he added reality to the philosophy by showing ever-diminishing sediment from the filled shore area outward to profundal parts of the basin.

The most effective promoter of the above concept was no doubt Dachnowski by his artistic diagram which appeared in the Ohio Journal of Science in 1912. Since then it has, throughout the years, wandered into textbooks and various other publications—it appeared again in a textbook released in 1955.

Errors Which Persist

All these publications are perhaps of little significance to the seasoned palynologist, but their influence in the training of young men should be considered. Errors which I made in 1931 are still being made. We still bore bogs of the "Weiher" type with full confidence and clutter up the literature with all sorts of explanations distilled from every source of glacial geology on origin of lakes. If there is something wrong with forest history, we propose later initiation of lake formation, persistence of ice blocks for thousands of years or more to prevent initiation of sedimentation until the spruce got tired of waiting and went merrily on its way northward. Such explantions are heralded with joy by the harassed worker, to give his truncated profile a respectable entrance into the scientific literature. Our young workers very frequently do not half realize the dynamite of the "Weiher" type of bog. Two years ago I was privileged to look at some Kodachromes of certain bogs which had been bored to study vegetational history. Open pools and "X marks the spot where we bored along the rim" were prominent in the pictures. Chances are nine to one that these bogs will yield truncated profiles.

Field Experiences

In 1941, Dr. Ira T. Wilson and I, in a study on methods, bored a bog and a lake from which profiles had previously been obtained and published, lacking the spruce-fir period. The bog still retained a wide central area of open water, and we bored in this area using a boat. The original report for the bog was depth 5½ feet—no spruce-fir, the first vegetation being pine-oak. Our boring in the deepest part—19 feet—showed 8 feet with spruce-fir. The original boring in the lake was 25 feet of peat, no spruce-fir, initial vegeta-

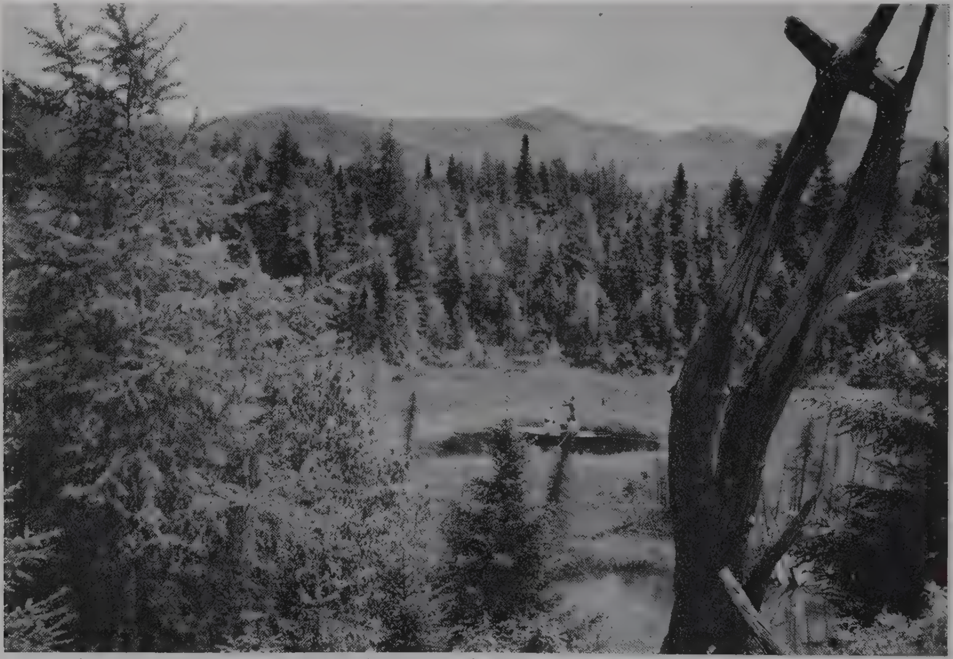

Fig. 5. Lac a Pit bog, Quebec, showing surrounding slopes. Boring being made from immobilized boat in open central pool.

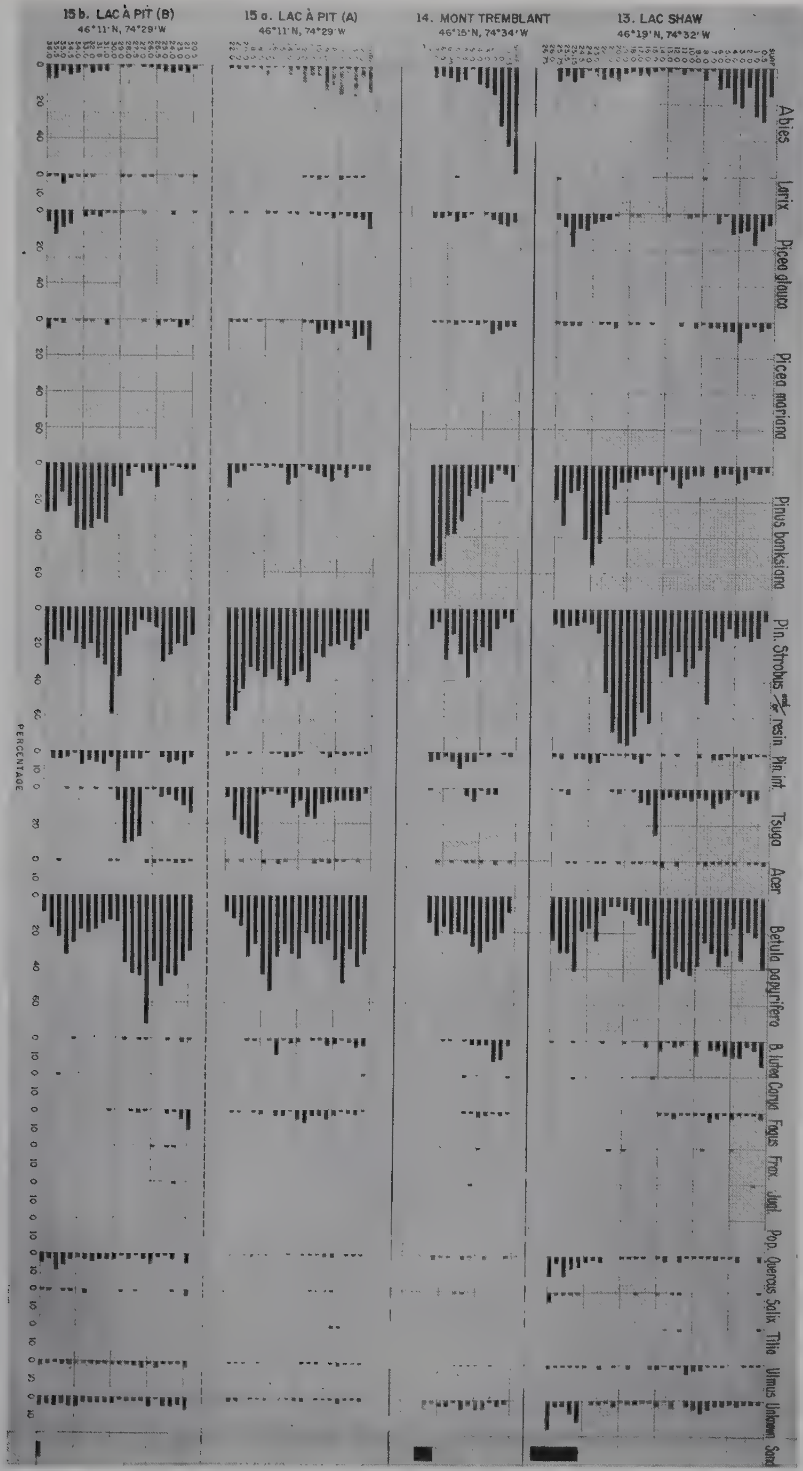

FIG. 6. Lac a Pit profiles A and B compared with two other profiles of the Mt. Tremblant region. Profile A—truncated. Profile B—early spruce-fir period included.

tion over 90% pine. Our boring—41 feet—gave 5 feet of spruce-fir.

In my Quebec work, I could not resist boring at the border of a 25 foot wide pool in each of two beautiful kettle bogs. Truncated cores resulted, and we had to repeat the borings to get the complete history, this time from a boat in the center of the pool (Fig. 5).

The extent of truncation of climatic and forest history will depend on the Wisconsin substages where one works. Tazewell in Indiana has a very long spruce-fir period (8 to 10 foot-levels) and so this period appears, at least in part, over a wider expanse of a lake basin than in Cary or Mankato time. In Mankato, especially, the spruce-fir period is rather short, and in Quebec the rapid Timiskaming retreat and the Cochrane halt (Q-1 and Q-2) are the two important climatic changes which are omitted where borings are made at the *edge* of central open pools.

Lake basins are very variable in depth as well as in contour, and sampling must take this into consideration. Trial borings are the only way to locate the deepest part or parts of a basin. For that reason it is wise to select if at all possible, smaller bogs, preferably of the kettle type. Several sampling soundings usually indicate the general trend of slope and so direct to the deepest part, for it is not infrequent to find the deepest part off center. In 1946, I worked in central Michigan and at Blue Lake near Muskegon (Fig. 4B), I bored a small bog of oval surface outline. I bored in the approximate center to a depth of 14 feet. Superficial examination of the lowest level under the microscope showed the spruce-fir period wanting. The following day the bog was visited again and extensive soundings showed that the deepest part was near one side. A boring through 18 feet of peat had the spruce-fir period in four foot-levels. When surrounding moraines or rock outcrops slope sharply towards a bog, forming a funnel, only the deepest part of the

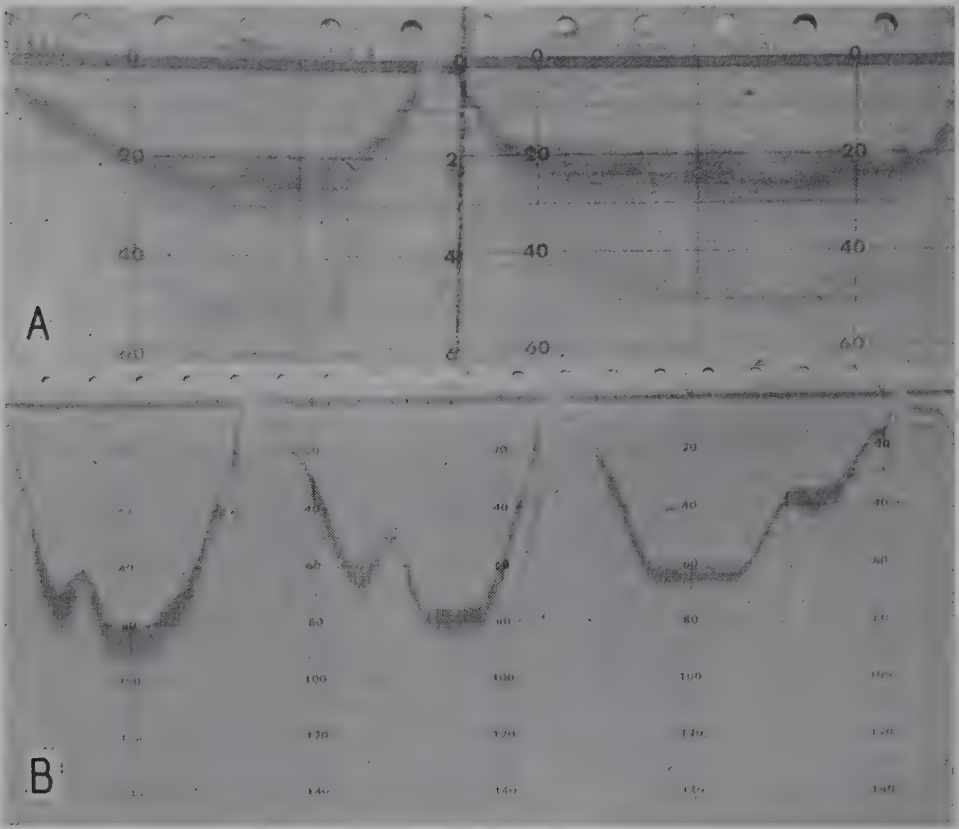

FIG. 7. Bendix depth finder recordings of two Quebec lake basins. A.—Lac aux Atocas, box-like basin with steep sides and level floor. B.—Lac Monroe, irregular basin with a number of depressions.

funnel, which may not exceed 25 feet in diameter, will record the whole forest history. This was the case at Lac a Pit bog (Figs. 5 and 6) and also at Lac des Plages bog, both in Quebec. Only once have I encountered a basin (Lac aux Atocas, Quebec) with sharp side slopes and a flat bottom, like a dishpan. See Figure 7. In such a basin, one could perhaps obtain a complete profile in most locations of the basin. Borings in lakes do not free the worker from the basin problems, and it is not so easy to make soundings in lakes as in bogs. These dynamics of initial filling apply to deep basins as well as to shallow basins, forcing extreme caution in the sampling of *any* bog or lake. I agree with Dr. Deevey that raised bogs ought to be avoided.

So much for the simple basins. Let us now consider the deeper lakes with complex bottom configuration such as Winona and Tippecanoe (121 feet) in Indiana, and Third Sister, Douglas (200 feet), and Middle Fish lakes in Michigan, where the bottom is a complex series of hills and valleys. In the work done in collaboration with my friend Ira T. Wilson, who labored hard and long on transect borings across the length and width of lakes, pollen profiles gave excellent service in determining the manner and time of filling. Time is used here in the sense of correlation with forest history. We found it was not only the deepest part of such a basin, nor the whole profundal area, but every deeper part of the profundal area which accumulated sediment from the beginning. Thus in the same lake, a 30-foot depth recorded the entire forest history as well as an area to a depth of 87 or over 100 feet, provided these represented depressions. A master profile from the deepest section can be used as a check for all other profiles from the same lake. Lake borings pose a problem because the necessary trial soundings from a boat are time-consuming. Ira Wilson did it in a most efficient manner the hard way. At the Mt. Tremblant Biological Station we determined bottom configuration with the aid of a Bendix depth finder (Fig. 7). All that was required was to place the recording part of the machine in the water and then by rowing or with the aid of a motor cross the lake. A moving stylus in contact with moving sensitized carbon paper sketched the contour of the bottom, in response to ultrasonic vibrations reflected from the basin walls and floor. For lake work, especially for deep lakes, I consider such a machine an absolute necessity. The bottom configuration of even large lakes can be sketched in a few hours. To a certain degree the depth of sediment is also indicated. Even this instrument is not absolutely fool-proof, for where large accumulations of sediment are present the basin configuration may be only faintly indicated. This may be a serious problem in older basins like the Indiana lakes, where sediments cover deeply the original floor of the basin.

It is my fond hope that my field experience of twenty-five years may be of some service to young American palynologists by way of saving them disappointment and wrong conclusions.

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THE ECOLOGICAL RELATIONS OF SYMPATRY IN *PLETHODON DUNNI* AND *PLETHODON VEHICULUM*

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The problems of interspecific competition and the ecological relationships of sympatric species have long attracted the attention and interest of students of ecology and speciation. Darwin believed that since competition occurs between organisms with similar needs, and since related organisms have the most similar needs, then closely-related organisms are likely to display the strongest interspecific competition. Gause (1934) carried this theme one step further and suggested that two species with similar ecology cannot live in the same area. Crombie (1947) re-examined the entire problem of interspecific competition and decided that Darwin's conclusions were entirely correct. He held that closely-related species which occur in the same area will compete when the population ratios are high enough and that one species will eliminate the other or an ecological separation will occur.

Lack (1944), after extensive study of competition in birds, held the view that closely-related species either frequent different regions or different habitats, or, when they live in the same place, eat mainly different foods. Two species of European cormorant which occupied the same habitat were found by Lack (1945) to differ markedly in food and nesting sites.

Extensive work on interspecific competition has been carried on by Park and others (Allee *et al.* 1949) by use of laboratory cultures composed of mixed populations of two or more species. In general it has been found that in these "mixed species" cultures one species will eliminate the other but the initial size of the population of each species and the exact condition of the medium determines which species will be eliminated.

Using a very different approach to the problem, Elton (1946) found that the average number of species per genus in small communities was much smaller than the same ratio in large faunal areas. This difference, he believed, was due to ecological competition between species of the same genus. However, Williams (1947) applied his index of diversity and the logarithmic series to Elton's data and other data of the same type and concluded that there were more species per genus in small communities than would be expected in a random distribution of species per genus. Williams believed that on the average the advantages of environmental suitability outweight the disadvantages of an increased number of competitors with similar habitat needs.

A consideration of the several lines of evidence indicates that, to be undisputed species, two populations must have reproductive isolation as well as separable physical differences. Gene mutations, which are the basis of the variation between species, cause not only morphological differences but also physiological differences in thresholds, tolerances, optima, pessima, etc. If physiological factors are expressed through behavior in the basic habitat requirements of the species, and it is unlikely that there would be no physiological differences between species, then it is improbable that two species would have exactly the same basic habitat requirements.

Even if these requirements are not genetically controlled beyond broad generalities, it seems improbable that two species would have identical habitat requirements. Mayr (1943), Dobzhansky (1941), and others have pointed out that the usual method of vertebrate speciation is by geographic isolation. Since the environments, both physical and biotic, of two incipient species are not identical, it is apparent that the adjustments of each race to its environment will be different, and thus two behavior patterns will be produced. By the time speciation is complete, identical habitat requirements for the two species are highly improbable.

If either of the methods of speciation and origin of habitat requirements discussed in the previous two paragraphs is true then several hypothetical habitat distribution patterns are possible: (1) If one or more of species A's requirements are met only in habitat X and one or more of species B's requirements are met only in habitat Y, then the two species cannot coexist in the same habitat and no competition is involved. (2) If species A's requirements may be met in one manner in habitat Z and species B's met in another way in habitat Z, the two species may coexist but there is no competition. (3) Species A and B may differ in some requirements but overlap in one or more. As the populations increase the overlapped factor will come into increasingly short supply and competition will increase proportionally. Variations, both cyclic and irregular are, however, to be expected. These fluctuations may directly or indirectly reverse the competition dominance. Thus species A and B may coexist in habitat Z in a state of dynamic equilibrium with competition present in any degree of intensity. (4) The requirements may be the same as in the last-discussed pattern; however, the population size may be inhibited more by density-independent factors and intraspecific competition than by interspecific competition. In this case the overlapped factor may never become critically scarce. Thus the two species may coexist with slight or no interspecific competition.

Occurring in western Oregon are two closely related species of salamander, *Plethodon dunni* and *Plethodon vehiculum,* which not only occupy the same general region but exist most abundantly in the same ecosystem. *Plethodon vehiculum,* somewhat smaller in size than *dunni,* ranges northward through western Washington where *dunni* does not occur, while *dunni* is found in southwestern Oregon where *vehiculum* is absent. Both species inhabit a rather wide area in west-central and northwestern Oregon. For these reasons an investigation of the sympatric relations of these two species was undertaken to attempt to determine which of the foregoing hypothetical distribution patterns most closely fits the facts. The plan of work involved a comparative field study of the environments of the two species and concurrent laboratory investigations of food habits, optima and extremes of habitat tolerances. Since both species of salamander occur abundantly in the Coast Ranges west of Corvallis, Oregon, most of the field work was carried on in this region.

The terms community, habitat, and ecosystem have been used by various authors to denote different concepts. To avoid confusion the definitions proposed by Dice (1952) will be used here. The community refers to the multi-specific assemblage of ecologically related organisms. The ecosystem is the total of the community and its habitat. The microstand is a small concrete example of the ecosystem. Several different sources have been used for identification of the fauna and flora. The following are authorities used for the nomenclature of the various groups: plants (Gilkey 1951), insects (Essig 1946), and the remainder of the invertebrates (Pratt 1935).

The statistical tests and procedures used are adapted from an unpublished outline of an introductory course in biological statistics developed by Dr. Jerome C. R. Li, Professor of Mathematics, Oregon State College. In every statistical test the five per cent level of significance was used.,

I wish to express my appreciation to Dr. Robert M. Storm, Department of Zoology, Oregon State College for his constant assistance and encouragement throughout the work on this problem. Also, my thanks are extended to Dr. Francis C. Evans, Institute of Human Biology, University of Michigan, for his critical reading of the manuscript and many helpful suggestions.

DESCRIPTION OF ECOSYSTEM

Habitat

Plethodon dunni and *Plethodon vehiculum* occur together most abundantly in the ecosystem which may be designated as "Rocky outcrop-Talus slope." This ecosystem is very frequent in the maturely-dissected Coast Range of Oregon where streams have cut deeply through the underlying rock. Slopes are usually steep, even precipitous. In this region are numerous rocky outcrops, usually with slopes of talus debris at their bases. Due to the salamanders' moisture requirements the occupied rocky outcrops are in close proximity to streams, springs, and seepages. The surfaces of the slopes are usually covered with several inches of a duff composed of fir and hemlock needles and twigs, though leaves of deciduous trees and shrubs may form an important part of the duff in some microstands. Soils are thin and very rocky. The underlying and exposed rocks are fine-grained sandstones and shales containing a multitude of small, interconnecting cracks.

The general climate of the geographic ranges of these two plethodontids varies somewhat with latitude and elevation. Table I presents a comparison of various climatic extremes of weather stations (U. S. D. A. 1941) within the ranges of *Plethodon vehiculum* and *Plethodon dunni.* This comparison indicates the general climatic extremes tolerated by the two species.

TABLE I. Macroclimatic extremes within general ranges of *P. vehiculum* and *P. dunni*

	TEMPERATURE, °F				Growing Season
	Minimum Jan. Av.	Maximum July Av.	Maximum	Minimum	
vehiculum.....	35.6	66.7	105	−15	147-273 days
dunni.........	36.6	86.7	106	−20	140-269 days
	PRECIPITATION, IN.				
	Max. Mo. Ppt. Av.	Min. Mo. Ppt. Av.	Maximum total ppt.	Minimum total ppt.	
vehiculum.....	20.68	0.22	128.58	39.43	
dunni.........	25.09	0.45	129.47	39.43	

Some altitudinal variation may be expected because *Plethodon vehiculum* ranges from about sea level to 2,500 feet elevation and *Plethodon dunni* ranges from about sea level to 3,000 feet elevation.

Shade in all of the occupied microstands was found to be very heavy, caused either by topographic shading or shadows cast by the shrub and tree layers.

The general seasonal climatic progression of the habitat is usually as follows. During the winter the high rainfall and relative humidity keeps all surfaces and subsurfaces very moist. Occasional short periods of very cold, dry weather occur. The temperature gradually rises during the spring but rainfall and relative humidity remain high. The summer months with the accompanying drought period witness a very rapid decrease in moisture in the habitat. By the latter part of August the duff is dry and the substratum to a depth of several feet has dried appreciably. The only moist areas present are those adjacent to springs, seepages, streams, and very deep in the rock outcrops. The lowered temperatures and onset of the fall rains very rapidly change the habitat conditions so that by October and November the relative humidity is very high and the temperature nearly the same as in winter.

Associated Biota

The floral members of the ecosystem may be divided into four strata: tree, shrub, herb, and moss. The tree and shrub strata, whose chief importance to the salamanders consists in the production of shade, are characterized by Douglas fir (*Pseudotsuga taxifolia*), western hemlock (*Tsuga heterophylla*), grand fir (*Abies grandis*), western hazel (*Corylus rostrata*), Oregon grape (*Berberis aquifolium*) and salmon-berry (*Rubus spectabilis*). A varied, though not abundant, assemblage of plants is found in the herb stratum. *Stenanthium occidentale, Maianthemum bifolium, Anemone deltoidea, Tellima grandiflora, Viola glabella, Synthyris reniformes,* and *Mimulus alsinoides* are most often present. Mosses are usually abundant and varied.

The assemblage of animals to which the two species of salamander belong is essentially a cryptozoan fauna although the birds and some mammals are not cryptozoic forms. By far the most abundant are the collembolans and mites. Every bit of moist debris turned over in the ecosystem reveals many individuals. Spiders, millipeds, centipedes, and symphilids, though not so abundant as collembolans and mites, tend to occur at greater depths in the ground by using holes, cracks, and crevices in the rocks. The amphibians *Dicamptodon ensatus, Rhyacotriton olympicus,* and *Ascaphus truei* are most abundant on the wet margins of the ecosystem, while *Aneides ferreus, Taricha granulosa,* and *Ensatina eschscholtzii* occur most frequently in the more xeric portions. The subsurface runways of shrew-moles (*Neurotrichus gibbsi*) frequently criss-cross the rock slides. These tunnels appear to be used extensively as runways for shrews, mice, and salamanders.

FIELD RESULTS

Substratum Comparisons

Four degrees of substratum moisture content were readily identified in the field work: (1) damp—earth or duff only discolored with moisture; (2) moist—minute water droplets individually visible on substratum; (3) wet—a thin water film covering substratum; (4) very wet—puddles of water or water flowing over substratum. The frequency distribution of *Plethodon dunni* and *Plethodon vehiculum* in relation to these four substratum ranks is shown in the histogram in Figure 1. It appears that *Plethodon vehiculum* prefers a moist substratum while *Plethodon dunni* prefers a wet substratum; however, the latter is not so limited to one category as is the former. Field observations indicate that when the relative humidity in the ecosystem is high *Plethodon dunni* may frequently be found in a moist substratum, but as the humidity falls this species is quite closely limited to a wet substratum. Although both species can swim and exist for considerable lengths of time immersed in water, they avoid any cover having as a substratum puddles or running water.

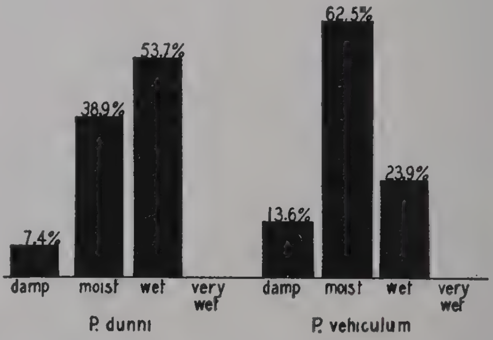

FIG. 1. A comparison of the distribution of *P. dunni* and *P. vehiculum* by degrees of substratum moisture content.

Temperature Comparisons

During the field observations on the two plethodontids the temperatures of the sites of collection of 110 *dunni* and 81 *vehiculum* were taken. These temperatures were taken by placing a thermometer in the position of the salamander and so measuring the substratum temperature and thin layer of air above the substratum. These temperatures were then pooled with regard to season, age, and sex for each species. Table II represents a comparison of the temperatures selected by the two species. It was found that the variance of the temperatures selected by *dunni* (6.31) was significantly different from the variance of the temperatures selected by *vehiculum* (10.61). Since the variances were significantly different the use of Student's *t*-test for comparison of the means would be invalid. When the populations have different variances, the statistic

$$t = \frac{(\bar{x}_1 - \bar{x}_2) - (\mu_1 - \mu_2)}{\sqrt{\frac{s_1^2}{N_1} + \frac{s_2^2}{N_2}}}$$

follows approximately Stundent's *t*-distribution with *n* degrees of freedom, where

$$n = \frac{\left(\frac{s_1^2}{N_1} + \frac{s_2^2}{N_2}\right)^2}{\frac{\left(\frac{s_1^2}{N_1}\right)^2}{N_1 + 1} + \frac{\left(\frac{s_2^2}{N_2}\right)^2}{N_2 + 1}} - 2$$

It should be noted in Table II that the mean temperature selected by *Plethodon dunni* (10.4°C) was not significantly different from the mean temperature selected by *Plethodon vehiculum* (10.4°C). From these statistical tests it seems that there was no difference in the temperature preferred by each species but that *vehiculum* was less exacting in its temperature requirements than was *dunni* although the extremes of the temperatures selected were nearly identical.

TABLE II. Comparison of temperature selections

Plethodon dunni		*Plethodon vehiculum*	
Temperature	*Frequency*	*Temperature*	*Frequency*
4°C	1	5°C	4
6	1	6	2
7	16	7	13
8	10	8	5
9	20	9	13
10	9	10	9
11	12	11	7
12	14	12	5
13	15	13	6
14	9	14	5
15	2	15	6
17	1	16	3
		17	2
		19	1

$\bar{x}_1 = 10.4°$ $\bar{x}_2 = 10.4°$
$s_1^2 = 6.31°$ $s_2^2 = 10.61°$
5% level of significance.
$t = 0.19$ with 207 degrees of freedom (not significant).
$F = \frac{s_2^2}{s_1^2} = 1.68$ with 80 and 109 degrees of freedom (significant).

Relative Humidity Comparisons

When collecting 89 *dunni* and 71 *vehiculum* the relative humidity of the site of collection was determined for each individual by means of a dew-point apparatus. These data were pooled for each species with regard to season, age, and sex. Table III presents a comparison of these data for the two species. As with temperature, the *F*-test indicates that there was a significant difference between the variances of the relative humidities selected by *dunni* (108.98) and those selected by *vehiculum* (219.76). There was no difference between the mean relative humidity selected by *dunni* (92.4%) and the mean relative humidity selected by *vehiculum* (89.1%). It appears that the preferred relative humidities of the two species were the same but *vehiculum* had a greater tolerance of non-preferred relative humidities than did *dunni* even though the extremes were identical.

TABLE III. Comparison of humidity selections

Plethodon dunni		*Plethodon vehiculum*	
Humidity	*Frequency*	*Humidity*	*Frequency*
63%	2	63%	2
67	1	69	3
69	1	73	6
71	1	77	1
73	2	78	4
77	1	82	2
78	2	83	1
82	1	87	1
87	1	88	8
88	6	89	1
92	10	92	1
94	13	93	3
95	1	94	19
96	5	96	4
98	1	98	1
100	40	100	14

$\bar{x}_1 = 92.4\%$ $\bar{x}_2 = 89.1\%$
5% level of significance.
$s_1^2 = 108.98\%$ $s_2^2 = 219.76\%$
$t = 1.47$ with 62 degrees of freedom (not significant).
$F = \frac{s_2^2}{s_1^2} = 2.02$ with 88 and 70 degrees of freedom (significant).

LABORATORY RESULTS

As a supplement and check on data from field studies concurrent studies were conducted in the laboratory. An attempt was made to analyze separately and in various combinations some of the major ecosystem factors both at the extremes and within the extremes of these factors.

Temperature Comparisons

In order to compare the time-temperature relationships of the two species of salamanders, the following apparatus was arranged. Five flasks were placed on a long metal plate. One end of this plate was resting on a small electric heater. Thus, a temperature on this plate could be found from about 20°C (room temperature) to 75°C. Each flask contained several millimeters of water on the bottom and the flasks were adjusted to the various positions on the metal plate where the desired temperatures were found. These temperatures were 26°, 28°, 32°, 36°, and 40°C. An adult salamander was then placed in each flask and the elapsed time till non-response to stimulation was noted. At 0°C and —1°C the flask was placed in an ice water bath (carefully regulated by additions of small pieces of ice, and the length of time till non-response to stimulation was noted. The specimens of *dunni* ranged from 48 to 65 mm in snout-vent length and the specimens of *vehiculum* from 46 to 57 mm. Three individuals of each species were used at each temperature. A graph showing a comparison of the results is given in Figure 2. The graph line is fitted through the mean time until non-response of the three individuals of each species used at each temperature.

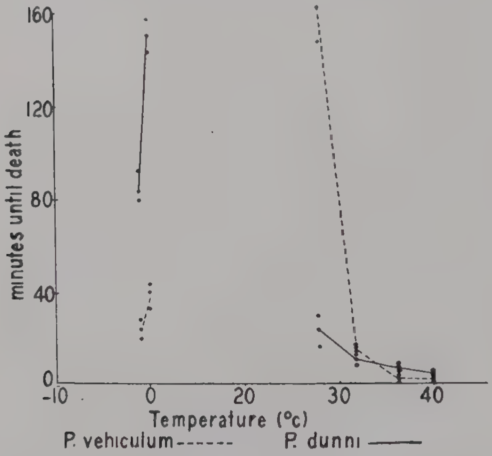

FIG. 2. A comparison of the time-temperature relationships of *P. dunni* and *P. vehiculum.*

Relative Humidity Comparisons

An experiment comparable to the time-temperature study was carried out investigating the comparisons of the time-relative humidity relationships. Air was saturated by bubbling through water, dehumidified by passing through an appropriate concentration of H_2SO_4. The dehumidified air had any acid fumes removed by passing through bone charcoal, and was then passed through the flask containing the experimental salamander. The entire apparatus was immersed in a water bath at a constant temperature of 12°C. A comparison of the results is presented in the graph in Figure 3.

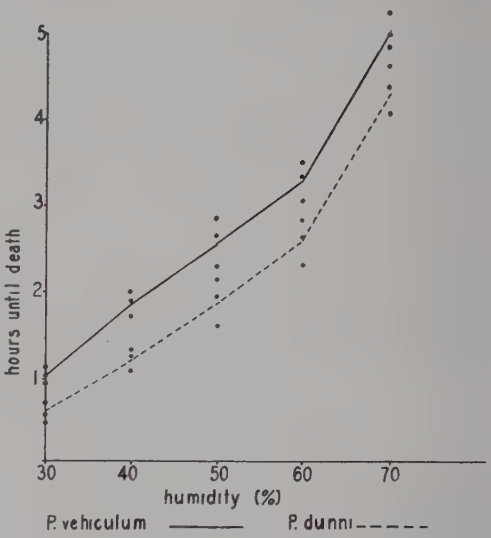

FIG. 3. A comparison of the time-relative humidity relationships of *P. dunni* and *P. vehiculum.*

Temperature-Relative Humidity Relationships

An attempt was made to determine what effect temperature and the presence of the opposite species had on the relative humidity selected by each species. The apparatus used was in essence the same as that used in the time-relative humidity relationships experiment. However, instead of confining the individuals in a flask, they were put into a circular trough into which jets of variously dehumidified air were simultaneously introduced. In this manner, individuals were free to select the desired humidity as the several factors were modified. The entire apparatus was cooled to 2°C, six salamanders put into the relative humidity gradient track, and the apparatus and water bath allowed to warm up to room temperature, 19°C. This warming required about six hours so that the individuals had ample time to adjust to the changing conditions. The relative humidity selected by each individual was determined with a dew-point apparatus five minutes after each temperature check point, 3°, 7°, 11°, 15°, and 19°C, was reached. The entire process was repeated three times; once for each species separately and once with both species present in the gradient track.

Table IV presents the raw data from these experiments. The data are the relative humidities selected by each individual. Table V presents the analysis of variance calculations. In this analysis of variance, the denominators of the *F*-tests were determined in the following manner. The error mean square was used to test the significance of the three-factor interaction. Since this was not significant, these two mean squares were combined to give a pooled mean square of 71.12 with 99 degrees of freedom. This pooled mean square was then used to test the significance of the B-C and A-C interactions. The mean square of this latter interaction, being significant, was then used as the denominator of the remaining *F*-tests. Although there were several other methods by which the *F*-values might have been determined, the procedure followed tended to minimize the possibility of accepting a false hypothesis. The only significant variation was found to be due to the A-C interaction, that is, due to the two species and species mixtures. Tukey's Test (Tukey 1949) was then applied to the means of the four levels of the A-C interaction as indicated in Table VI. The mean which was significantly different from the other three was that of *Plethodon vehiculum* when in the gradient track with *Plethodon dunni.* This appears to indicate there is no significant difference normally between the relative humidities selected by the two salamanders but that the presence of *Plethodon dunni* in the higher humidity tends to force *Plethodon vehiculum* to select lower humidities than are preferred.

Table IV. Original temperature—humidity relationship data. A_1—humidities selected by *dunni* under all experimental conditions; A_2—the same for *vehiculum.* B_1—humidities selected by all salamanders at 2-4°C regardless of crowding; B_2—the same at 6-8°C; etc. C_1—humidities selected by the salamanders when both species were together; C_2—same when only one species was present.

	C_1 (both sp.)					C_2 (1 sp. at time)				
°C	B_1 2-4	B_2 6-8	B_3 10-12	B_4 14-16	B_5 18-20	B_1 2-4	B_2 6-8	B_3 10-12	B_4 14-16	B_5 18-20
A_1 dunni	100	100	100	83	95	100	89	100	85	85
	73	80	78	100	85	70	100	92	100	100
	90	79	88	85	100	80	78	100	100	100
	87	100	90	100	98	75	85	88	100	100
	85	95	100	90	100	90	92	100	92	88
	100	93	80	85	100	83	100	98	85	98
A_2 vehiculum	60	78	60	80	88	85	86	89	88	100
	74	85	78	85	74	71	100	94	100	98
	89	83	80	80	82	90	83	100	90	90
	71	61	75	73	95	72	95	92	93	100
	80	80	60	75	90	94	84	100	92	100
	87	78	80	90	90	86	78	85	100	98

Table V. Analysis of variance 5% level of significance

Variation due to:	Sum of squares	Degrees of freedom	Mean square	F	Remarks
Replication...	126.57	5	25.31	0.024	NS (5, 1 d.f.)
A...........	1,320.03	1	1,320.03	1.236	NS (1, 1 d.f.)
B...........	1,536.45	4	384.11	0.360	NS (4, 1 d.f.)
C...........	1,241.64	1	1,241.64	1.163	NS (1, 1 d.f.)
A x B.......	160.56	4	40.14	0.038	NS (4, 1 d.f.)
A x C.......	1,068.03	1	1,068.03	15.017	S (1, 99 d.f.)
B x C.......	646.95	4	161.74	2.274	NS (4, 99 d.f.)
A x B x C....	15.04	4	3.76	0.056	NS (4, 95 d.f.)
Error........	6,399.10	95	67.36	.....	....
Total.....	12,514.37	119	105.16	.....	....

Tabie VI. Tukey's test, applied to the data of Tables IV and V

$$\text{Least Significant Difference} = t\propto\sqrt{\frac{2s^2}{N}}$$

N = number of observations in each treatment
t = t − value at ∝
s_2 = error mean square
∝ = level of significance used (5%)

$$LSD = 2.04\sqrt{\frac{2(67.36)}{30}}$$

$$LSD = 4.284$$

$\bar{x}_{a_2c_1} = 78.13$) difference = 12.97, significant
$\bar{x}_{a_2c_2} = 91.10$) difference = 0.20, not significant) difference = 0.67, not significant
$\bar{x}_{a_1c_1} = 91.30$) difference = 0.47, not significant
$\bar{x}_{a_1c_2} = 91.77$

Comparison of Laboratory and Field Data

Although, as indicated in Table II, the mean temperatures selected by the two plethodontids are not significantly different, *Plethodon vehiculum* has a greater tolerance for non-preferred temperatures than does *dunni.* This same difference is indicated in the time-temperature relationship graph in Figure 2. However, this same graph indicates that *Plethodon dunni* has a greater tolerance of low temperatures than does *vehiculum.* Much the same conditions exist with regard to relative humidity comparisons of the two species as is indicated in Table III and Figure 3. *Plethodon vehiculum* is more tolerant of low relative humidity conditions than is *Plethodon dunni;* however, very high relative humidities do not appear to affect either species adversely. Within the normal range of temperature and relative humidity conditions encountered by the two species, temperature does not significantly alter the relative humidities selected, as shown by Table IV. However, the presence of *Plethodon dunni* in the preferred habitats of *Plethodon vehiculum* may cause the latter species to select non-preferred but tolerated habitats. This competition may explain, at least in part, the differences in substratum distribution indicated in Figure 1.

Food

Since many students of interspecific competition believe that the food supply is the main factor in competition, a study of the comparative food habits of *Plethodon dunni* and *Plethodon vehiculum* should aid in clarifying their sympatric relationships. Thirty-six filled stomachs of adult *dunni* and 37 filled stomachs of adult *vehiculum* were examined. The specimens were collected together in the same microstands. A summary of the stomach contents is presented in Tables VII and VIII. *Plethodon dunni* consumes a much greater variety of foods than does *vehiculum.* Possibly correlated with the relative sizes of the two salamanders is the fact that *vehiculum* consumes more very small-sized forms, such as mites, then does the larger *dunni.* The higher mean number of items per *vehiculum* stomach is almost entirely due to the many minute collembolans consumed. Of the items having high frequency indices only the collembolans are consumed in large numbers by the two plethodontids. From these considerations it appears that collembolans are the most important food source of both *vehiculum* and *dunni.* If an arbitrary separation of primary and secondary food sources is made at the frequency (percentage) index of 10.00, the similarity of primary food sources or "staple" foods is readily apparent. Of the total of 16 "staple" items, 10 are shared by both species. And, of these shared items, all except staphylinid beetles and polydesmid diplopods are more frequent and possibly more important foods for *vehiculum* than for *dunni. Plethodon vehiculum* seems to have far fewer secondary food sources, 14, than does *dunni, 27.*

TABLE VII. *Plethodon dunni* stomach contents; frequency index = percentage of stomachs examined that contained the item

	Total items	Frequency	Items/stomach	Frequency index
Annelida	6	3	2.00	8.40
Gastropoda	8	4	2.00	11.20
Endodontidae	2	1	2.00	2.80
Zonitidae	3	3	1.00	8.40
Arionidae	4	1	4.00	2.80
Pauropoda	3	1	3.00	2.80
Isopoda	13	6	2.17	16.80
Chilopoda	1	1	1.00	2.80
Geophilidae	2	2	1.00	5.60
Diplopoda	6	3	2.00	8.40
Polydesmidae	10	6	1.67	16.80
Julidae	1	1	1.00	2.80
Scorpionida	2	2	1.00	5.60
Pseudoscorpionida	1	1	1.00	2.80
Araneida	7	5	1.40	14.00
Acarida	18	11	1.14	30.80
Phalangida	2	2	1.00	5.60
Aptera	1	1	1.00	2.80
Insect adult	1	1	1.00	2.80
Insect larva	14	8	1.75	22.40
Collembola	38	9	4.22	25.20
Sminthuridae	58	14	4.14	39.20
Isoptera	3	1	3.00	2.80
Ephemerida	1	1	4.00	2.80
Homoptera	1	1	1.00	2.80
Hemiptera	1	1	1.00	2.80
Coleoptera adult	14	10	1.40	28.00
Coleoptera larva	3	2	1.50	5.60
Staphylinidae adult	11	7	1.57	19.60
Elateridae adult	6	3	2.00	8.40
Rhyncophora adult	2	2	1.00	5.60
Scaphidiidae adult	23	2	11.50	5.60
Diptera adult	2	2	1.00	5.60
Diptera larva	8	3	2.67	8.40
Tipulidae larva	3	2	1.50	5.60
Empidiidae adult	3	1	3.00	2.80
Hymenoptera	7	4	1.75	11.20
Chrysididae	2	2	1.00	5.60
Formicidae	9	4	2.25	11.20

Mean number items/stomach, 8.36

TABLE VIII. *Plethodon vehiculum* stomach contents

	Total items	Frequency	Items/stomach	Frequency index
Annelida	24	6	4.00	16.20
Gastropoda	1	1	1.00	2.70
Haplotrematidae	1	1	1.00	2.70
Zonitidae	6	5	1.20	13.50
Isopoda	21	14	1.50	37.80
Chilopoda	1	1	1.00	2.70
Geophilidae	3	1	3.00	2.70
Diplopoda	1	1	1.00	2.70
Polydesmidae	6	5	1.20	13.50
Pseudoscorpionida	8	6	1.33	16.20
Araneida	29	14	2.07	37.80
Acarida	49	19	2.58	51.30
Phalangida	2	1	2.00	2.70
Insect adult	3	3	1.00	8.10
Insect larva	25	11	2.27	29.70
Collembola	459	15	30.60	40.50
Sminthuridae	78	16	4.87	43.20
Mecoptera	1	1	1.00	2.70
Coleoptera adult	10	10	1.00	27.00
Staphylinidae	7	4	1.75	10.80
Scaphidiidae	10	1	10.00	2.70
Elateridae larvae	3	2	1.50	5.40
Diptera adult	1	1	1.00	2.70
Diptera larva	1	1	1.00	2.70
Tipulidae	1	1	1.00	2.70
Lepidoptera larva	4	4	1.00	10.80
Hymenoptera adult	2	1	2.00	2.70
Formicidae	12	10	1.20	27.09

Mean number items/stomach, 20.84

In addition to the items listed, several stomachs of both species contained bits of plant remains and small amounts of sand and other inorganic debris. The role of these items in the diet is unknown, but they may represent accidents of ingestion while capturing the normal prey.

The similarity of the primary food sources of *vehiculum* and *dunni* would indicate that there may be rather strong competition for these items. However, since *dunni* has more numerous secondary food sources than does *vehiculum* the former species would be better able to survive periods of scarcity of the primary food sources than would *vehiculum.* That food scarcity may be tolerated quite readily is indicated by the remarkable resistance to starvation by both species. Seven adult *dunni and* 10 adult *vehiculum* were kept in a refrigerator at 12°C and approximately 95% relative humidity for 158 days without death. The very nearly optimum temperature and humidity conditions prevented the individuals from becoming torpid. In view of the extreme abundance and variety of the various food items available in the "Rocky outcrop-Talus slope" ecosystem it seems unlikely that food would ever become a strong factor in the competition between *dunni* and *vehiculum*.

Life History

No study of sympatric relationships is complete without some comparison of the life histories of the species involved. Unfortunately, little is known about the life history of either *Plethodon vehiculum* or *Plethodon dunni*. Furthermore, what meager knowledge is available is not derived from direct observation but mainly from indirect evidence. This is particularly true of the time, method, and type of reproduction.

Reproduction

As with most other forms of plethodontid salamanders, breeding in *vehiculum* and *dunni* is probably accomplished by the female picking up with her cloacal lips the spermatophore which has been deposited on the substratum by the male. The spermatophore is retained within the female's cloaca until the time of egg-laying. As the eggs pass through the cloaca fertilization occurs.

Apparently neither *vehiculum* nor *dunni* has a well-defined breeding season. Several female *vehiculum* found in January did not appear externally to be gravid but their cloacae contained spermatophores. Stebbins (1951) induced gravid females of both species to lay fertile eggs by use of pituitary implants. Since the possibility for breeding of these individuals in captivity was slight, viable sperm must have been present prior to the collection date, April. A cloacal smear of a female *dunni* collected in October showed sperm present. Furthermore, some males of both species show testicular enlargement at every season of the year.

The time, site, and method of egg-laying is fully as difficult to determine as is the time of breeding. Females of both species, which by external appearances seem to be fully gravid, have been found at all seasons of the year. As far as is known no eggs of *vehiculum* have been found in nature, and eggs of *dunni* have been found only once. On July 6, 1952 a grape-like cluster of nine eggs was found by the author. The female *dunni* found within a few inches of the cluster was flaccid but not emaciated, apparently having recently deposited the cluster. An attempt was made to hatch these eggs in a refrigerator. By September 10, mold, which had been flourishing on the cluster in spite of repeated fungicide treatments, caused the destruction of the final embryo.

This final embryo had a snout-vent length at the time of death of about 16 mm. Individuals of both species of this approximate sixe (13-22 mm) have been found during every season of the year, although they are most abundant during spring and fall. The foregoing considerations seem to indicate that egg-laying by both species may take place at any season of the year with possible peaks of activity in early winter and early summer. The reproductive rate of both species is apparently quite low for the ratio of these very small individuals to the total population of each species at any one time seems never to be higher than 1:20. This very low ratio, however, may be in part the result of these very small individuals being more secretive than the larger individuals. Presumably their small size would make them much more susceptible to desiccation so that a subterranean existence is necessary. Furthermore, at least two years are probably required for individuals of either species to reach sexual maturity. Apparently the females of both species usually reach sexual maturity at a snout-vent length of 40-44 mm as no gravid females were found smaller than this.

Mortality

As with most poikilothermic animals the physical environment, especially temperature and relative humidity, is apparently the most important factor affecting the mortality rate of both *vehiculum* and *dunni*. These plethodontids, in optimum conditions, may wander quite widely from the preferred habitat. However, if habitat conditions vary toward the pessimum, the salamanders must return to a tolerated environment or perish. Since these plethodontids are sluggish salamanders with rather low mobility, wandering far from a tolerated habitat brings about destruction. *Plethodon vehiculum,* as has been pointed out, is tolerant of somewhat higher temperatures and lower relative humidities than is *dunni*. This allows *vehiculum* to wander into adjacent microstands of the same or similar ecosystems especially during the warmer seasons. *Plethodon dunni,* being more tolerant of low temperatures, may wander away from the preferred ecosystem during the colder seasons if the humidity remains high. This lower temperature pessimum also allows *dunni* to be found at slightly higher elevations than *vehiculum*.

Data on predation must usually come from direct observation; therefore, data are meager. *Dicamptodon ensatus* specimens in captivity have eaten small and medium-sized individuals of both *vehiculum* and *dunni;* however, analysis of stomach contents of six adult *Dicamptodon* collected in the "Rocky outcrop-Talus Slope" ecosystem failed to reveal plethodontid remains. On one occasion a dipper (*Cinclus mexicanus*) was observed to capture either a *vehiculum* or *dunni* from among rocks by a small creek. A Steller's jay (*Cyanocitta stelleri*) was seen to capture a *dunni* from the surface of a talus slope. A freshly-killed *vehiculum* was found in a tunnel made by a shrew-mole (*Neurotrichus gibbsi*) and may have been killed by this insectivore.

Several other animals which may be predatory on *vehiculum* and *dunni* occur in the ecosystem. The carabid beetle *Scaphinotus* may feed on small plethodontids as may the scorpion *Uroctonus mordax*. The alligator lizard *Elgaria coerulea* and the garter snake *Thamnophis ordinoides* may also be plethodontid predators. The Canada jay (*Perisoreus canadensis*) and the shrews *Sorex trowbridgei and Sorex pacificus* would probably prey on the two species of salamanders whenever possible.

Cannibalism is apparently rather rare. The only recorded case is a female *dunni* consuming some of her recently-laid eggs (Stebbins 1951). Mixed colonies of both species have been maintained under starvation conditions in the laboratory without unexplained loss of small individuals.

Diseases and heavy parasitism have not been found in either species. The only exception is fungus infection. This, as previously explained, proved lethal to *dunni* eggs. A somewhat similar infection occurs on adult *dunni* which have been retained at relatively high temperatures in the laboratory. The growth, which first appears about the base of the tail, spreading interiorly and posterially, is invariably fatal. *Plethodon vehiculum* does not appear to be affected.

Population Characteristics

Although no detailed population studies were pursued, several items are of importance. The sex of 52 adult *vehiculum* and 74 adult *dunni* was determined by dissection. There were 11 male and 41 female *vehiculum,* 21 male and 53 female *dunni.* The chi-square analysis of these data gave the following values: *vehiculum,* 17.30 with 1 degree of freedom; *dunni,* 13.84 with 1 degree of freedom. Both were significantly different from the expected 1:1 ratio at the 5% level of significance. When these data were analyzed by season of collection the same significant results were obtained. This means that there are actually fewer males than females in the population, or that the males are more difficult to collect due to a somewhat different behavior pattern, or that a true hypothesis has been rejected in the chi-square analysis. The first possible conclusion, that there were actually fewer males than females, is probably valid, for there seems to be no other evidence either in the literature or in field observations that there is a difference between the behavior patterns of males and females which would affect the ease of their collection; and the third possible conclusion, that a true hypothesis was rejected, is rather unlikely at the 5% level of significance used.

Of 113 bits of cover under which *Plethodon dunni* was found only four concealed two individuals and one covered three individuals. *Plethodon vehiculum* was collected under 91 pieces of cover of which one piece of cover concealed two individuals and one covered three individuals. However, in terraria the individuals seemed to be distributed essentially at random when there were more items of cover than individuals. Thus it seems that there is little or no intraspecific social interaction, that is, no tendency for clumping or even spacing of individuals.

Although both species were found abundantly together in small areas, no instance of *vehiculum* and *dunni* being found together under the same piece of cover was noted. This tends to substantiate the conclusion drawn from the factorial analysis of the temperature-humidity relationships that the presence of *dunni* prevents *vehiculum* from occupying its preferred habitats.

Movements

Of prime survival value are the lateral and vertical movements made by each species in response to changing habitat conditions. A comparison of the monthly habitat distributions of *vehiculum* and *dunni* presented in Table IX. The category "Transient Habitats" includes such spots as under logs, planks, bits of bark, duff, and in wood. They are all essentially temporary types of cover used when either species is caught in the open by daylight. During the winter both species are very closely restricted to the talus slope portion of the habitat, but during late February and March when the temperatures begin to rise both species begin to wander extensively. This movement reaches its climax during the usually mild and humid month of April. At this time individuals of both species begin to appear abundantly among the stones immediately adjacent to streams and seepages. During early summer the daytime temperature rises toward the upper limits of tolerance and the relative humidity drops to the lethal points. In response to these habitat changes, both species become closely restricted to spots under stones near water or must crawl deeper into the talus or along cracks in the rock outcrops where the temperature is lower and the humidity higher. The existence throughout the year of a small population of both species very deep in the cracks in the rock may explain the paucity of breeding records of

Table IX. Monthly habitat distribution

Habitat		Species	Month												Total
			J	F	M	A	M	J	J	A	S	O	N	D	
In talus	0-3″ deep	dunni	12	4	5	4	12	0	0	0	0	3	5	11	56
		vehiculum	10	5	13	38	11	0	0	0	2	4	6	14	103
	below 3″	dunni	2	4	1	11	18	1	6	1	1	5	0	0	50
		vehiculum	1	9	8	8	6	5	3	2	1	0	0	2	45
Transient Habitats		dunni	0	8	3	22	8	3	0	0	0	2	17	1	64
		vehiculum	0	7	20	25	8	12	0	0	0	6	18	1	97
Under Rocks Near Water		dunni	0	0	6	7	32	31	8	11	13	0	0	0	108
		vehiculum	0	0	0	3	6	19	6	7	5	2	0	0	48

either species. The first heavy fall rains, usually in October, bring both plethodontids from their summer retreats and both species undergo the reverse of their spring movement. Though there is little difference in the movements undergone by each species, what differences do exist are important. *Plethodon vehiculum,* being tolerant of somewhat higher temperatures and lower relative humidities than is *dunni,* makes greater use of the "transient habitats." This undoubtedly reduces competition; however, it leads to a grave risk of being caught by lethal environmental conditions, for the weather conditions are notably variable during spring and fall when transient habitats are most frequently used.

Slope and Moisture Perception

Since the "Rocky Outcrop-Talus Slope" habitat is always a slope of varying degree and in view of the extreme importance of moisture to both species of salamander, a few simple experiments seemed necessary to determine their ability to perceive various degrees of slope and the presence of moisture.

Slope and moisture perceptions of the two species of plethodontids were tested by means of a large glass plate three feet long and two feet wide whose slope could be varied from 0° to 20°. Sixteen animals of each species were placed in the center of the glass, one at a time, eight with their heads upslope and eight with their heads downslope. The course taken by each animal was noted. The slope was then increased 5° and the experiment repeated. Table X presents a comparison of the results for each species. When no slope is present both species wander at random over the plate. When a slope of at least 5° was present the animals showed a significant tendency to move up-slope. The probability of *Plethodon dunni* going up-slope was 90% and the probability of *Plethodon vehiculum* going upslope was 95%.

The slope experiment was modified by the addition of wet cotton placed at one or both ends in order to test the moisture-perceptive ability of the two species. When no slope was present wet cotton was placed at one end. Then using a 10°

Table X. Chi-square analysis of slope-perception experimental results. Five percent level of significance, N = 16

Plethodon dunni

Angle of slope	End	Observed frequency	Theoretical frequency	Chi-square	Remarks
0°	A	8	8		Not
	B	8	8	0	Significant
5°	A	14	8		
	B	2	8	9	Significant
10°	A	14	8		
	B	2	8	9	Significant
15°	A	14	8		
	B	2	8	9	Significant
20°	A	12	8		
	B	4	8	4	Significant

Plethodon vehiculum

Angle of slope	End	Observed frequency	Theoretical frequency	Chi-square	Remarks
0°	A	7	8		Not
	B	9	8	.25	Significant
5°	A	13	8		
	B	3	8	6.25	Significant
10°	A	14	8		
	B	2	8	9	Significant
15°	A	14	8		
	B	2	8	9	Significant
20°	A	16	8		
	B	0	8	16	Significant

slope, wet cotton was placed at the upslope end and then the downslope end. The chi-square tests of the results are presented in Table XI. The upslope end in all tests is designated as end A. The theoretical probability in the chi-square tests of combined slope and moisture factors was the probability of each species going upslope as determined in the slope perception experiments. It appears from Table XI that when no slope was present both species wander at random to either end regardless of the presence of moisture. When moisture was present above their movements were not significantly different from those on a slope in a total absence of moisture. When moisture was present only down-slope there was a significant movement toward the moisture although there was still a rather pronounced upslope movement. Observations of experimental animals indicate that they may turn back upslope unless the animals have approached within about four inches of the down-slope moisture.

TABLE XI. Chi-square analysis of moisture-perception experimental results

Position of moisture		End	Observed frequency	Theoretical frequency	Chi-square	Remarks
Plethodon dunni						
No Slope	end A	A	8	8		Not
		B	8	8	0	Significant
Slope 10°	above	A	13	14.4		Not
		B	3	1.6	1.36	Significant
	below	A	14	1.6		
		B	2	14.4	4.00	Significant
Plethodon vehiculum						
No Slope	end A	A	9	8		Not
		B	7	8	0.25	Significant
Slope 10°	above	A	14	15.2		Not
		B	2	0.8	1.769	Significant
	below	A	5	0.8		
		B	11	15.2	23.20	Significant

N=16, 5% level of significance.

This pronounced upslope behavior and weak moisture-perception ability presents some interesting survival problems for both salamanders. During the late spring and early summer the margin of necessary soil moisture gradually recedes deep into the talus slopes and toward the streams and springs which are usually at the base of the slopes. Since both species of salamander have normally a strong tendency to travel up-slope, away from streams, and weak moisture-perception ability, these salamanders must stay near this receding moisture margin. If they wander more than a short distance from this margin they will move upslope which in the typical microstand would be away from necessary moisture. When the relative humidity is low this would cause rapid destruction of the individual. It is possible that this behavior pattern may constitute a strong mortality factor for both *Plethodon dunni* and *Plethodon vehiculum.*

SUMMARY AND CONCLUSIONS

1. A study was made of the ecological relations of *Plethodon dunni* and *Plethodon vehiculum,* which occur abundantly together in the "Rocky outcrop-Talus slope" ecosystem in western Oregon.

2. Field observations were made of the temperature, relative humidity, and substratum moisture at the site of collection, the sex of each individual found, and miscellaneous life history data. Concurrent laboratory studies were conducted to determine the food habits, time-temperature, time-humidity, and humidity-temperature-interspecific-crowding relations of each species of salamander. The slope and moisture perception of each species was tested.

3. Although *dunni* and *vehiculum* occur together in the same ecosystem, they differ somewhat in their habitat tolerances. *P. dunni* is tolerant of slightly lower temperatures and more moist substrata and *vehiculum* is tolerant of lower relative humidities and higher temperatures. However, the preferred conditions of temperature and humidity for the two species are not significantly different.

4. Competition between *dunni* and *vehiculum* seems very slight. The primary foods are similar but there are many differences in the secondary food sources. Food acceptable to both species seems to be sufficiently abundant in the ecosystem that this source of competition would rarely be critical. There is definite competition between the two species for spots having high humidities, with *dunni* tending to exclude *vehiculum.* However, in the ecosystem there are many more spots with proper humidities than there are salamanders, so competition for this requirement must be slight except during seasons of extreme dryness.

5. Both species have very weak moisture percepiton and, when released from other strong stimuli, have a pronounced tendency to move upward on any slope.

6. It appears that a relatively high mortality rate, due especially to adverse physical environmental conditions, keeps the total population of each species sufficiently low that the two sepcies may co-exist in the same habitat with slight or no interspecific competition.

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THE RELATION BETWEEN FREE SUGARS AND SEDIMENTARY CHLOROPHYLL IN LAKE MUDS[1]

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INTRODUCTION

It is commonly assumed that simple organic nutrients in lakes are utilized by microorganisms as quickly as they are formed by decomposition processes. The purpose of the present report is to suggest that this assumption is not valid for the free hexose and pentose sugars which occur in lake sediments (Vallentyne 1954). The important question of diagenesis of organic compounds in sediments has received our attention and we have developed a principle which indicates that diagenetic destruction of free sugars does occur in lake sediments.

The carbohydrates of lake sediments have been studied by a number of investigators (Sugawara 1939, Hutchinson and Wollack 1940, Kleerekoper and Grenier 1952), however most of the analyses have been for polysaccharides such as cellulose, hemicelluloses and chitin. Closely related to our work was the demonstration by Sugawara (1939) that reducing organic substances were extractable with hot or cold water from the sediments of Takasuka-numa, Japan. Theander (1954) has demonstrated that small amounts of free fucose occur in *Sphagnum* peat. So far as we are aware, free sugars have never been isolated from sediments in pure form.

MATERIALS AND METHODS

Collection of samples

The first sample used for sugar analysis was collected with a 9-inch Ekman dredge (12 m depth) from Lower Linsley Pond, Conn., in April 1952. This sample was stored in the dark at 4°C for two weeks before an aliquot was removed. The aliquot was mixed with ethanol until the concentration of the latter reached 70%.

Surface mud samples were collected with a 6-inch Ekman dredge on June 27, 1952, from the following Connecticut lakes: East Twin Lake, Lake Quassapaug, Lake Quonnipaug, Lake Waramaug and Lower Linsley Pond. Samples were mixed with ethanol (final concentration about 70%) at the time of collection. The samples were stored in flasks at 4°C until analyzed, except for a two week period when they were transported from New Haven to Kingston.

Sediment core samples from Bethany Bog, Conn., were collected with a Hiller boror in May 1952. Dr. D. A. Livingstone collected these samples for us. The samples were stored without preservative in the dark at 4°C until July, when aliquots were removed and mixed with ethanol.

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[1] The work reported here formed part of a thesis submitted by J. R. Vallentyne to the Graduate School of Yale University, in partial fulfillment of the degree of Doctor of Philosophy. We are indebted to G. Evelyn Hutchinson, who suggested that sediments be analyzed for sugars.

Analyses

Sugars were analyzed by the chromatographic method of Bidwell, Krotkov and Reed (1952). The amounts of sugars are given as mg sugar per kg dry weight of ethanol insoluble sediment (e.i.s.), *i.e.* in terms of the dry weight of sediment left after extraction. The true dry weights were probably higher by about 2-5%. Results are accurate to within 5-20%, depending on concentration. The accuracy of the method has been checked in two ways. In the first case, one sediment sample which had been previously extracted for sugars, was re-extracted and analyzed again. Free sugars were present in the first extract (11.5 mg glucose per kg dry weight e.i.s.), but not in the second. This indicates that extraction was complete (> 90%); that free sugars did not arise during extraction and concentration as a result of slow breakdown of alcohol-insoluble polysaccharides; and finally that contamination is not the source of the free sugars. For the second test a sediment extract was divided into two halves. Known amounts (25 μg) of seven sugars were added to one half and the other half was left unchanged. The extracts were both deionized with Amberlite IR-100 and Amberlite IR-4B exchange resins (unlike all other free sugar analyses reported on here). Recovery was quantitative (90-110%) for sucrose, glucose, galactose, fructose and arabinose. Losses up to 50% occurred for ribose and xylose. This loss may have been due to the use of the IR-4B exchange resin.

Analytical treatment of the April sample from Lower Linsley Pond was as follows:

(a) An aliquot of the combined water and ethanol extracts was used for the determination of free sugars.

(b) Another aliquot of the combined water and ethanol extracts was hydrolyzed with 3N HCl at 100°C for five minutes. The hydrolysate was deionized according to the method of Bidwell, Krotkov and Reed (1952) and then analyzed to give a measure of free sugars plus sugars released by hydrolysis.

(c) The ethanol- and water-insoluble fraction of the sediment was hydrolyzed in three volumes of 0.25 N HCl at 100°C for one hour. On neutralization a large precipitate formed (presumably ferric hydroxide) which was filtered off and washed. The filtrate was deionized and then used for the determination of sugars.

The sedimentary chlorophyll results from Bethany Bog are those given by Vallentyne (1955). Sedimentary chlorophyll refers to the complex of chlorophyll degradation products found in lake sediments.

RESULTS

Surface sediments

Table I lists the results of sugar analysis of the April sediment sample from Lower Linsley Pond. The values for free sugars are peculiar in two respects: the total free sugar content was nine times that found in a June sample (see below) from the same lake, and secondly this is the only Connecticut sample in which free sucrose and free fructose have been found. Hydrolysis of the ethanol- and water-soluble fraction liberated some xylose and ribose in addition to the glucose and fructose which resulted from the breakdown of sucrose. Absence of fructose in the hydrolysates (except for that originating from sucrose and free fructose) indicates an absence of fructosans which would have been broken down under these conditions.

TABLE I. Free sugars and sugars released by acid hydrolysis of sediment from Lower Linsley Pond, Connecticut. Results are expressed as mg sugar per kg dry weight of ethanol-insoluble sediment. A concentration of 6 mg per kg was just detectable

Sugar	ETHANOL AND WATER SOLUBLE		Ethanol and water insoluble
	Free	After hydrolysis	After hydrolysis
Sucrose	214	0	0
Glucose	191	301	29
Fructose	272	382	0
Galactose	0	0	29
Arabinose	0	0	202
Xylose	0	12	58
Ribose	0	12	29

Table II lists the free sugar contents of the surface sediments collected in June. The lakes are arranged in order of decreasing glucose content of the sediment. No relation was apparent between the depth of sampling and the free sugar concentration. Note however that there is a parallel between the concentrations of the two hexoses (glucose and galactose), but no corresponding relation among the pentoses, nor between any hexose and any pentose. There is no disagreement between Tables I and II with regard to free arabinose and free ribose. If these sugars had been present in the same concentration in the April and June samples they would not have been detected in the analysis of the April sample. The April and June samples differed slightly in free galactose content, as shown by a comparison of Tables I and II. The discrepancies between results from the April and

TABLE II. Free sugars in Connecticut lake sediments. Concentrations are given as mg sugar per kg dry weight of ethanol-insoluble sediment. A concentration of 1 mg per kg was just detectable

Sediment source	Depth (m)	Ignitable matter (%)	Glucose	Galactose	Arabinose	Xylose	Ribose	Total free sugar
L. Linsley Pond......	12.0	24.2	61	9.5	1.0	0.0	1.0	72.5
Lake Waramaug.....	9.5	20.4	37	4.0	5.5	7.5	1.0	55.0
Lake Quonnipaug....	9.5	32.8	25	2.5	2.5	0.0	0.0	30.0
Lake Quassapaug....	11.0	25.6	24	2.0	2.0	6.0	1.0	35.0
East Twin Lake.....	13.0	11.9	13	2.0	2.0	4.0	2.0	24.0

June samples may have been due to differences in time, location or method of sampling.

All the lakes under study have been examined for a variety of physico-chemical variables by Deevey (1940). In comparing the data presented in Table II to those given by Deevey, a relationship was found to exist between the free hexose content of the surface sediments (sampled in June 1952) and the average summer chlorophyll content of the seston (measured in 1937-39 by Deevey). When making such a comparison it is better to express sugar concentrations in terms of a unit ignitable matter rather than a unit dry weight. When the former mode of expression is used, the concentrations are independent of changes in the rate of inorganic sedimentation. The points for all five lakes gave a good fit to a straight line when the sugar concentrations were given as mg per kg dry weight, but this graph is not shown (because of its deceptiveness). The relation between sedimentary hexoses and seston chlorophyll is shown in Figure 1, with hexose concentrations given as mg per kg ignitable matter. Straight lines were fitted to the data from four lakes by regression analysis. The data for East Twin Lake were purposely excluded because the dredge failed to penetrate the compact sediment of this lake more than an inch or two, whereas it penetrated at least 6 inches into the sediments of the other lakes. The data for East Twin Lake are shown in Figure 1 only for purposes of comparison. It is evident from Figure 1 that there is a direct relation between sedimentary hexoses and seston chlorophyll. This relation may be fortuitous. Future and more extensive work is needed to determine whether the direct relation can be rigidly accepted. For the purpose of the arguments given below it will be assumed that the relationship is not due to chance alone. It should be stated however that more recent work on Ontario lake sediments has shown that the free sugars vary both qualitatively and quantitatively with the sampling location.

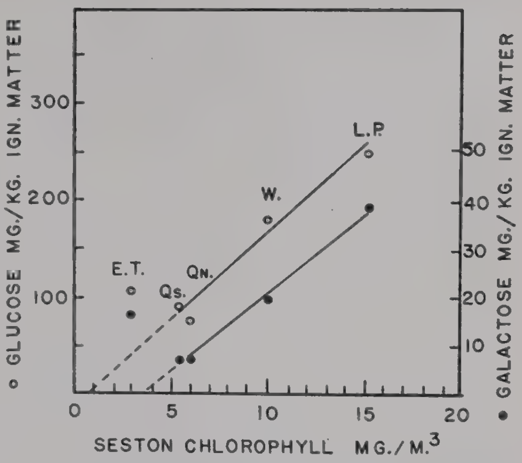

FIG. 1. Mg free glucose and galactose per kg ignitable matter in the sediment, plotted against average summer seston chlorophyll (data from Deevey 1940). LP, Lower Linsley Pond; W, Lake Waramaug; Qn, Lake Quonnipaug; Qs, Lake Quassapaug; ET, East Twin Lake. Open circles, glucose; closed circles, galactose.

Subsurface sediments

Having shown that free sugars were present in the surface sediments of lakes, the next step was to examine subsurface sediments. A sediment profile was taken from Bethany Bog, Conn., on the bog mat about 20 m from the area of open water. Samples were taken at meter intervals. We failed to penetrate sediments beyond 14.75 m depth. Below the 12-m level the samples were composed of silt-clay, but all higher levels were rich in ignitable matter. A study of the diatoms in the profile (Patrick 1954) has revealed four phases in the development of this lake:

(a) Oligotrophic: 14.75—13 meters
(b) Eutrophic: 12—9 meters
(c) Transitional: 8—7 meters
(d) Dystrophic: 6—0 meters

The samples for sugar analysis were taken from 12—7 m inclusive, *i.e.* all were deposited by a eutrophic or moderately dystrophic lake. The concentrations of free sugars in these samples are given in Table III. The important point is that although the concentrations were low, some free sugar was invariably present. Glucose content was maximal at the 9-m level where a high concentration of carotene has also been found (Vallentyne unpublished). Galactose was found only at the 8- and 7-m levels, but may have been present in the deeper samples in lower concentrations. The occurrence of galactose only in the transitional zone suggests that it may have originated from bog plants.

TABLE III. Free sugars in the 7-12 meter interval of the Bethany Bog profile. Concentrations and amounts detectable as given in Table II

Depth (m)	Glucose	Galactose	Total free sugar
7	5.0	1.0	6.0
8	8.0	1.0	9.0
9	11.5	0.0	11.5
10	7.5	0.0	7.5
11	1.0	0.0	1.0
12	2.0	0.0	2.0

The age of the Bethany Bog sediments was roughly estimated by comparing the pollen zonations of Deevey's profile (Deevey 1943) from Bethany Bog with the radiocarbon-dated levels of the pollen zones present in Upper Linsley Pond sediments (Flint and Deevey 1951). On this basis the sediments in the 7-12 m interval were estimated to be 5,000 to 9,000 years old. The presence of free glucose in sediments of this age does not necessarily suggest great stability of glucose, since the glucose may have been formed after deposition of the sediment.

A principle of diagenesis

The exact use of biochemical fossils to determine the abundance and kind of past life depends on the assumption that the concentrations of the fossil compounds have remained unchanged since the time of deposition. It has therefore been of importance to the present work to develop a principle which would give an unbiased measure of the amount of post-depositional change. The principle, although quite obvious, has never been clearly stated for molecular ratios so far as we are aware, although it has been applied to atomic ratios to indicate the relative rates of destruction of two atoms. The C/N ratio is often used in this sense. The principle is given below:

Given: two compounds, A and B, unrelated in structure and property, not known to occur in the same molecule and produced only by organisms. Assuming that equal rates of decomposition are unlikely, if the ratios A/B are identical at two or more sediment levels, than neither A nor B has changed in *absolute* concentration during the time interval between the two levels, provided that the ratio A/B in the organic matter sedimented has remained unchanged.

Three properties of the principle may be noted:

(a) The principle is logically consistent within itself and retains this consistency in spite of any data that appear to contradict it.

(b) The basis of the principle lies in the truth of the assumption. If the assumption can be disproved for two compounds then the principle does not apply to them. The truth of the assumption is rendered likely because the given compounds must be dissimilar in structure and property.

(c) If A is quantitatively transformed into A′ or B to B′ the principle may still be applied.

Figure 2 shows an attempt (which may not be legitimate) to apply the principle to the 12— 7 m interval of the Bethany Bog profile. Free glucose (mg/kg ignitable matter) is plotted against sedimentary chlorophyll (units per g ignitable matter) with the data presented as a scatter diagram. If there had been no diagenetic destruction of glucose and sedimentary chlorophyll then the same linear relation as found between sedimentary hexose and seston chlorophyll would be expected, with the straight line cutting the Y-axis near the origin. This is clearly not the case. Any line fitted to the data would cut the Y-axis well below the origin. The results indicate a decrease in the ratio of glucose to sedimentary chlorophyll. Three possible explanations are apparent:

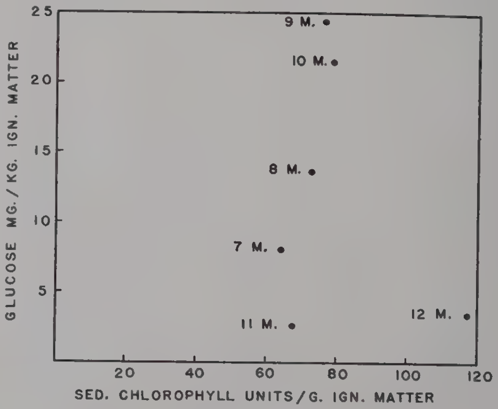

FIG. 2. Mg. free glucose per kg ignitable matter plotted against sedimentary chlorophyll units per g ignitable matter for the 7-12 meter interval of a profile from Bethany Bog, Conn.

(a) sedimentary chlorophyll has increased after deposition,

(b) free glucose has decreased after deposition,

(c) both (a) and (b) have occurred but the rate of (b) has been greater than that of (a).

Both (a) and (c) must be disregarded because it is unlikely that dark synthesis of chlorophyll can occur to any extent in a deposited sediment. Since the samples were limited to those taken from eutrophic and moderately dystrophic sediments the possibility that succession has influenced the glucose/sedimentary chlorophyll ratio has been minimized. We are left with the conclusion that glucose has been destroyed. It is also likely that sedimentary chlorophyll was being destroyed at the same time as glucose, only at a slower rate. We have no direct data bearing on this question.

If the rate of destruction of glucose were proportional to time then one would expect the lowest glucose/sedimentary chlorophyll ratios in the oldest sediments. This was true of the 11- and 12-m samples, but not of the others. Similar diagrams have been made for glucose against carotenoids with the same results (Vallentyne unpublished), however the possibility of post-depositional synthesis of carotenoids, as well as sugars, cannot be disregarded. The fact that the glucose/sedimentary chlorophyll ratio did not regularly decrease with depth may suggest that diagenetic destruction of glucose is dependent on factors other than time. In fact, the low glucose content of all samples (relative to surface sediments) indicates that the major reduction in glucose concentrations occurred shortly after deposition. It would be interesting to analyze a near-surface profile for free sugars.

Discussion

Questions arise about the origin of free sugars in lake sediments and their mode of preservation. Let us first consider their possible origins. The free sugar contents of plant tissues have been investigated by Bidwell, Krotkov and Reed (1952). These workers found that free sucrose was invariably present in fresh plant tissues, and free galactose always absent. It is apparent from the results given above that all the free sugars of sediments (with the possible exception of the April sample from Lower Linsley Pond) could not all have arisen directly from the free sugars of plants. The average glucose content of the algae (Chlorophyta excluded) investigated by Bidwell, Krotkov and Reed (1952) was 200 mg per kg dry weight. Members of the Chlorophyta had a higher sugar content than other algae. This figure (200 mg per kg) is identical with the amount of free glucose found in the April sample from Lower Linsley Pond. If the sediment concentrations are referred to a unit ignitable matter (which is a more reasonable comparison) then it is found that the April sample had four times as much free sugar as a sample of fresh algae (Chlorophyta excluded) of equal weight. On an ignitable matter basis the sediments from the other lakes contained about the same amount of free glucose as would be expected for fresh algae (Chlorophyta excluded). A direct origin of the free sugars of sediments from the free sugars of algae is therefore unlikely for two reasons: the relatively high concentrations of free sugars in sediments, and secondly the differences between free sugars commonly found in algae and those found in sediments. Two other possible sources should be considered: that the sediment sugars originated from the free sugars of higher plant tissues or else from the breakdown of polysaccharides of either algae or higher plants. The former possibility may be true for some of the sediment sugars (sucrose, glucose, fructose), but could not be true for others (notably galactose). On the other hand the hydrolysis of polysaccharides *in situ* can reasonably be expected to occur in sediments.

The problem of explaining the "preservation" of free sugars in lake sediments is serious when one considers that many microorganisms remove the last traces of free sugar when this is added to their growth medium. One must remember, however, that the only data we have to work with in sediment analyses are concentrations, and these tell nothing of the stability of free sugar molecules. The sediment concentrations reflect a steady state between recruitment of free sugar molecules (*e.g.* from sinking plankton and polysaccharide hydrolysis) and emigration (*e.g.* breakdown of sugars during bacterial metabolism). The free sugar molecules themselves may be and probably are unstable in sediments, *i.e.* have half-lives of the order of a few hours, days or weeks. If this is the case (and it must certainly be true for that fraction of sedimentary free sugar which is present in living micro-organisms) then it is absurd to speak of sugars as biochemical fossils in any sense of the word. On this interpretation our data suggest that formation of free sugar is faster than breakdown. If some factor other than a carbon source were growth-limiting to mud bacteria *in situ,* then a pile-up of free sugar might be expected. Whether this reasoning is valid only future experiment will tell.

On the other hand if free sugar molecules are reasonably stable in sediments (*i.e.* have half-lives of 5 years or more) then it is conceivable that they might derive this stability by virtue of location in micro-areas of mud which are relatively inaccessible to bacterial or free-enzyme attack. There are many micro-locations in mud about which very little is known with regard to biochemical stability. It should be emphasized that in speaking of free sugars in sediments we are really referring to the free sugars of alcoholic extracts of sediments.

SUMMARY

1. The following free sugars were identified in alcohol extracts of Connecticut lake muds: sucrose, glucose, galactose, fructose, arabinose, xylose and ribose. Glucose was the most abundant free sugar. It occurred in concentrations of 13-191 mg per kg dry weight of ethanol-insoluble sediment.

2. A direct linear relation was found to exist between free sedimentary hexoses and summer seston chlorophyll in the surface muds of four Connecticut lakes.

3. A principle of diagenesis was developed and applied to data for sedimentary free sugars and sedimentary chlorophyll in a profile from Bethany Bog, Connecticut. It is concluded that free sugar is destroyed at a faster rate in lake muds than sedimentary chlorophyll.

4. The free sugars of sediments do not all directly arise from the free sugars of plants, but rather appear to be at least partly breakdown products of polysaccharides.

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DEVELOPMENT OF AEDES (DIPTERA: CULICIDAE) AT FORT CHURCHILL, MANITOBA, AND PREDICTION OF DATES OF EMERGENCE[1]

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INTRODUCTION

A program of biological and control studies on biting flies has been conducted since 1947 at Fort Churchill, Manitoba (Hocking *et al.* 1950; Twinn *et al.* 1948; Twinn 1950; Twinn *et al.* 1950). The planning of biting-fly control programs for military areas in the Canadian north (Brown *et al.* 1951; Twinn *et al.* 1950) has indicated the need of more basic information on the ecology, development, and behavior of pest flies. The effectiveness of large-scale chemical control programs depends largely on the proper timing of applications of the insecticide. During the planning stage especially, information on population peaks and on seasonal variations in insect behavior related to the environment is important when control operations are limited to one or two applications. In the fly-infested areas of the north, where chemical control for the protection of small field parties is not practical, some interest has also been shown in the possibility of using periods of relative inactivity of certain pest flies for carrying out field operations.

Studies on the behavior of the immature stages of mosquitoes in subarctic environments have been described, Haufe, to be published, a). Coordinated studies during the same period (1949-52) were designed to ascertain the rate of development of mosquitoes in relation to subarctic environments. The possibility that there are two relations involving the environment of developing stages of mosquitoes is discussed in this paper on the basis of continuous seasonal observations on pools in a natural mosquito habitat. These relations may exist (i) between rate of development and thermal conditions of the environment and (ii) between thermal conditions of the environment and meteorological phenomena. Mathematical relations between development and environmental conditions have been suggested by Blunck (1923) and Bodenheimer (1927) for insects on the basis of environmental air temperatures. Apparently use of mathematical devices in estimation of development of mosquitoes has not been described previously.

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[1] Contribution No. 3286, Entomology Division, Science Service, Department of Agriculture, Ottawa, Canada. The results herein reported were obtained by the Entomology Division in a program of studies on the biology and control of biting flies being carried out on behalf of the Defence Research Board, Canada Department of National Defence, and with the co-operation of that organization and other agencies.

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Accurate prediction of adult insect emergence depends on the variation that may be expected (i) in assessment of effects of environmental factors on rate of development, and (ii) in measurement of meteorological and edaphic factors that are known to influence rate of development. The development of dry-land insects is usually subject to considerable, and frequently to extreme, degrees of variation; but organisms developing in water are less subject to extreme fluctuations in the environmental factors that may be difficult to measure. The object of the studies described in this paper was primarily to determine variabilities in those factors that may be important in estimating the periods of emergence of northern mosquitoes.

Mosquitoes found in the Fort Churchill area include the following species: *Aedes impiger* (Walk.) (= *A. nearcticus* Dyar; Vockeroth 1954), *A. nigripes* (Zett.), *A. punctor* (Kirby), *A. hexodontus* Dyar, *A. pionips* Dyar, *A. excrucians* (Walk.), *A. flavescens* (Müller), *A. campestris* D. & K., *A. cinereus* Mg., and *A. communis* (Deg.). All these species except possibly *A. communis* habitually bite man in this locality. Although not considered a pest in the area under observation, *A. communis* was selected for study for several reasons: (i) It was the only species to be found easily in pure or nearly pure colonies in the number of pools necessary for a comparative study on thermal environment. (ii) It was the most abundant species in the immature stages; studies in individual pools might be conducted with large samples of populations since the larvae often exceeded 25,000 in a single pool. (iii) The species tolerates large variations in several edaphic factors, a characteristic that enhances the value of observations on the development of a species in various types of environment (Haufe 1952). (iv) Studies on behavior of *A. communis* larvae indicated that patterns of behavior related to geophysical factors may influence the dependence of rate of development on certain thermal conditions of the environment (Haufe, to be published, a). (v) Comparative studies on the patterns of behavior of species listed as serious biters indicated that the 'blacklegged' species of *Aedes* (*A. impiger, A. nigripes, A. punctor, A. hexodontus, A. pionips,* and *A. communis*) were qualitatively the same in this respect; the only interspecific variation in pattern of behavior appeared to be in the degree of aggregation (Haufe, to be published, a). Aggregations were not observed for *A. excrucians, A. campestris, A. flavescens,* and *A. cinereus;* but the numbers of immature stages of these species in individual pools were possibly too small to exhibit noticeable aggregations. Some species such as *A. campestris* and *A. flavescens* selected shallow, muddy pools less than two inches deep. In this type of habitat the horizontal and vertical temperature gradients common to deeper pools (Haufe, to be published, a) may be insignificant or even non-existent.

Of the species mentioned above, the 'blacklegged' group of *Aedes* was of primary economic importance in the north where the protection of military camps was concerned. Our investigation of the possibility of early prediction of emergence of mosquitoes was chiefly directed toward these species. Although preliminary reports (Hocking *et al.* 1950; Twinn *et al.* 1948) have described the general life cycle of these mosquitoes, it should be emphasized that the 'blacklegged' group in the Subarctic is univoltine. Beckel (1953) found that eggs recovered from pools following the summer period of oviposition would not hatch before they were subjected to low temperatures. Eggs hatch very quickly and larval development is rapid however in the spring with the first exposure of eggs to open water at pool margins. These species therefore have a diapause in the egg stage that has the effect of telescoping the life cycle of post-hatching stages into short periods of mass-development. Consequently the emergence of each species is marked by sudden increases in the adult mosquito population and the species also emerge in close succession to cause the rapid build-up of hordes of mosquitoes over a period of usually not more than six weeks each summer. These characteristics of the mosquito life cycle are advantageous in the solution of problems of prediction on the basis of meteorological and environmental conditions.

Appreciation is expressed to W. N. A. McLean and J. A. Armstrong, Survey Assistants, Veterinary and Medical Entomology Unit, Ottawa, for assistance in the field work in 1951 and 1952, respectively, and to Lieut. K. R. Van Skike, Preventive Medicine Company, United States Army, for assistance in 1951; to G. F. Kennedy and other members of the Meteorological Division, Canada Department of Transport, Fort Churchill, Man., for co-operation in supplying special meteorological data and services; to Dr. C. R. Twinn, Head, Veterinary and Medical Entomology Unit, Ottawa, for valuable assistance; to Prof. F. P. Ide, University of Toronto, for advice in planning the work and reading the manuscript; and to Dr. F. J. O'Rourke and Dr. J. J. R. McLintock, Veterinary and Medical Entomology Unit, Ottawa, and others for reviewing the manuscript and making suggestions.

METHODS

Biological Method

The methods employed in the field studies had three objectives: (i) to investigate the effects of meteorological factors on the thermal conditions of a pool in so far as they influence the development of mosquito larvae, (ii) to describe mathematically the rate of development of a species of mosquito in relation to the thermal conditions of the environment, and (iii) to compare the rates of development of the pest species of mosquitoes in the area.

For (i) the studies were conducted in nine pools. These varied in size, shape, depth, and location, sinces it was important to measure the maximum variation in mosquito development that might be attributed to physical characteristics of the pool and to edaphic factors of surrounding terrain. The pools formed a series from the completely exposed type that is common on the tundra to the type partially sheltered by vegetation that is characteristic of the transition between tundra and Boreal forest. The sites used for these studies are described in detail in a previous paper (Haufe, to be published, a). The pools used for all phases of the study were typical of either tundra or forest-tundra transition in a permafrost area.

The meteorological conditions were recorded at the study site and supplemented when necessary by records from the weather station at Fort Churchill. Meteorological data included continuous records of air temperature, sunlight, humidity, wind chill, and wind speed. The thermal condition of the pool was recorded as the daily average temperature taken at a depth of one inch below the surface of the water in the deepest part of the pool. Experience indicated that for most temperature equipment accuracy of measurement was greater at one inch than at lesser depths. Continuous recordings of pool temperature were made in some of the pools by multiple-pen-type temperature recorders (Taylor, Series 75 J)[4] fitted with mercury-actuated bulbs and extensions; in other pools, maximum daily variations in temperature were recorded by maximum and minimum thermometers.

For (ii) the studies were restricted to seven pools, two in 1951 and five in 1952. In 1951 the investigation of the effects of thermal conditions of the environment on rate of development was combined with behavior studies of immature stages of *A. communis* (Haufe, to be published, a) in the same pools. Behavior patterns of mosquito larvae were related to their thermal environment; therefore the combined studies were arranged primarily to assess the accuracy with which mathematical "time x temperature" components[5] of development might be corrected for the effects of daily patterns of behavior. The behavior studies on the species had indicated (i) the temperature preferendum and (ii) an estimate of the amount by which pool temperatures in an insolated sector exceeded recorded one-inch temperatures.

Larvae and pupae were free in the pools during the major part of their development. When the pupae became more numerous than the larvae, a cage was erected near the middle of the pool in a position at which the water temperature equalled or nearly equalled the average one-inch temperature. Pupae that appeared to be ready to emerge were dipped into the cage daily; mature pupae of *A. communis* are easily distinguished by their flashing, white ventral parts. When the white scales are formed on the abdominal sterna of the nearly developed adult, the light is reflected from the white scales through the pupal skin. As the pupa works downward in the water in daylight a flash of white is discernible with each flexion of its abdomen. Usually pupae could be caged as little as a day before emergence of the adults by this method. The risk in this procedure is that density-dependent factors may influence the rate of development in a cage. We experienced high mortalities among larvae in overcrowded cages in previous surveys of northern mosquitoes. Gillies and Schute (1954) have also described some effects of overcrowding in laboratory cultures of mosquitoes. For this reason approximately 50 pupae only were added to the cage each day following the appearance of white ventral parts on the abdomen. We considered this procedure to be adequate since the form of distributions obtained for frequency of emergence in individual pools was nearly normal in all cases with consistent skewness to the right. Adults were removed from the cages daily at the same hour. Males and females were segregated and frequency curves of emergence were drawn for each sex. The period of development was considered to be the time from the first appearance of open water in the pool to the peak of emergence for the adults trapped in the cage. This arbitrary delimitation was based on practical availability of meteorological data for widespread areas. Communication in arctic and subarctic areas in Canada is maintained primarily by light aircraft equipped with skis or pontoons. The break-up of ice along the shorelines of lakes and ponds is particularly important in the spring season in the briefing of pilots on military and civilian missions. The appearance of open water in pools and lakes is carefully documented geographically at aviation forecast offices for large areas from reports of pilots that arrive daily at both major and minor supply bases serving military and civilian outposts. The arbitrary selection of first appearance of open water to delimit the beginning of mosquito development is practical therefore from a meteorological point of view. Furthermore, the delimitation is biologically adequate since univoltine species of mosquitoes in the Subarctic hatch immediately with the thawing of pool borders (Haufe, to be published, a).

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[4] Taylor Instrument Companies, Rochester 1, New York, U.S.A.

[5] The "time x temperature" component of development is the theoretical product of time (in units) and temperature (in units) necessary for development to the adult after the thawing of the pool in spring.

The development of *A. communis* was studied in 1952 by the same general procedure and with the same type of equipment. The selection of pools was modified, however, to get a series of developmental "time x temperature" components of various magnitudes. This was accomplished by selecting single pools at intervals of about a week, *i.e.*, the first pool was the one in which open water appeared earliest during the spring thaws, the second was one in which open surface water appeared approximately a week later, etc. The "time x temperature" components of pools selected in this manner were different on the basis of seasonal summations of meteorological conditions. The combined studies on the development of *A. communis* provided data for comparing rate of development with environmental temperatures under natural conditions.

For (iii) a study was carried out in 1952 by a procedure similar to that for (ii) except that the study was designed to compare rates of development of the species of mosquitoes common in the area. The development of each species was studied in at least three pools having different thermal characteristics, two to establish a relation between rate of development and environmental temperature and a third to provide a check on the reliability of the results. The data were treated in the same manner as for (ii).

STATISTICAL METHOD

The interdependence of meteorolgical factors that contribute to the environment was recognized in all correlations. Conrad and Pollak (1950) recognized the need for this approach in solving climatological problems and reviewed methods and concepts that are useful primarily in representing climatological phenomena. They have pointed out the advantages and disadvantages of certain methods in relation to various geophysical problems. The environment of immature mosquitoes must be recognized as a complex of interdependent dynamic factors and this view plays an important part in the selection of a suitable statistical method. The coefficient of correlation (r) and its probable error (F) were used to evaluate the relation between meterological factors and the water in mosquito pools. Although the probable error does not meet with complete satisfaction as a test of significance under certain conditions, it has the advantage of accommodating the rare observations that may be termed *force majeure*. The probable error therefore is useful in testing correlations within extremely dynamic situations such as the natural environment of mosquitoes. The chief hazard in the analysis of relations between major factors in natural environments is the inevitable influence of unexpected inter-relationships that have to be considered as unavoidable accidents in the design of the investigation. Rare and unexpected events that cause discontinuities in the data from a field study affect the use of the probable error less than other tests of significance.

On the basis of confirmation by physical reasoning or other independent evidence "six times the probable error" has been accepted as the "rule of thumb" for avoiding false conclusions in correlations between natural elements. It is equivalent to odds of 10,000 to 1 as compared with 20 to 1 for "three times the probable error." "Three times the probable error' is accepted in the correlation of natural elements only when it is supported by other independent evidence. This criterion is not too severe when the purpose of the study is kept in mind. Individual geophysical factors may be expected to have little value in the practical prediction of mosquito development unless the correlation is very high.

Where X, T, Y, Z represent the variations in pool temperature (°F), air temperature (°F), daily sunshine (hours), and wind chill (kg-cal/metre^2/hr) respectively:

Coefficient (r) between pool temperature and air temperature is

$$r_{XT} = \frac{1}{n} \cdot \frac{\Sigma XT}{\sigma_X \cdot \sigma_T}$$

Probable error of the coefficient is

$$F = 0.6745 \times \frac{(1 - r^2_{XT})}{\sqrt{n}}$$

r is significant for rigorous purposes only if it is greater than 6 times the probable error.

Coefficient (r) between pool temperature variations (X) and air temperature variations (T) at constant daily periods of sunshine is

$$r_{XT.Y} = \frac{r_{XT} - r_{XY} \cdot r_{YT}}{\sqrt{(1 - r^2_{XY})\ (1 - r^2_{YT})}}$$

In Figures 1-3 inclusive the lines representing the *regression equations* are combined with the dot chart to provide visual indication of the degree of correlation. For example, in Figure 1 in which X and T represent pool temperature and average daily air temperature respectively, the deviations of X and T from the arithmetic mean are plotted in pairs on a cartesian coordinate system with origin (0, 0). The points (X, T) might be scattered in such a way that they cover the quadrants of the coordinates with greater uniformity as the number n of the pairs of deviations is increased. In this case no correlation exists between X and T. However in Figure 1, the dot diagram shows a crowding of the points into the first and third quadrants indicating a linear proportionality. This proportionality is represented by a straight line $T = bX$ that passes through the origin and is best fitted to the point cloud.

If T should be an analytic linear function of X, then $T - bX$ would be exactly zero. In this investigation this is not valid and the value of b must be determined so that the difference $T - bX$ becomes as small as possible. Since only the absolute magnitudes of the deviations, and not their signs, play any role in this problem, b should be chosen so that the sum of the squares of $T - bX$ is minimum. The condition is fulfilled if

$$\frac{d}{db}\Sigma(T - bX)^2 = 0,$$

and

$$b = \frac{\Sigma XT}{\Sigma X^2} = \frac{(^1/n)\ \Sigma XT}{(^1/n)\ \Sigma X^2}$$

The equation $T = bX$ contains the arbitrary assumption that X is the independent variable; but this assumption is not valid for this problem under the circumstances of the study. For instance, if X is the independent variable the air temperature (T) is considered to be influenced by the ground temperature and hence also by the pool temperature (X). In other words we know that radiation of heat takes place from the ground to the air during the night. But we also know that warm air masses moving over cold ground transfer heat to the ground and hence also to the pools. For the latter physical condition T must be considered the independent variable. Since there is a continuous alternation of these two physical conditions from day to day in the relationship between air temperature and ground surface temperature, two arbitrary assumptions must be included in the relation between the two variables, namely that either X or T may be the independent variable depending on the physical circumstances. Therefore the mathematical considerations must be more specific and besides the relation $T = bX$ it is also true for this problem that

$$X = b^1T$$

$$\text{and } b^1 = \frac{(^1/n)\ \Sigma XT}{(^1/n)\ \Sigma T^2}$$

If the standard deviations (σ) are considered

$$\sigma_X = \sqrt{\frac{\Sigma X^2}{n}} \quad \text{and} \quad \sigma_T = \sqrt{\frac{\Sigma T^2}{n}}$$

and

$$b = r\frac{\sigma_T}{\sigma_X},\ b^1 = r\frac{\sigma_X}{\sigma_T}$$

b and b^1 are the *regression coefficients* and the *regression* equations are

$$T = r\frac{\sigma_T}{\sigma_X}X$$

$$\text{and } X = r\frac{\sigma_X}{\sigma_T}T.$$

The two regression equations mentioned above are represented in Figure 1 by the two straight lines. The smaller the angle between the two regression lines the higher is the degree of association and the greater is the value of the correlation coefficient r. If $r = \pm 1$ the two regression lines concide while if $r = 0$ one line is identical with the X-axis $(T = 0)$ and the other with the Y-axis $(X = 0)$. The correlation coefficient between air temperature and pool temperature is high. From Figure 1 the small angle between the regression lines verifies the strong association. The combination of the regression equations with dot charts in Figures 1-3 provides additional means of evaluating the relationships between pairs of factors in nature that do not meet the rigorous test of 6 times the probable error.

EFFECTS OF METEOROLOGICAL CONDITIONS ON ENVIRONMENT OF THE MOSQUITO

Factors

Any useful method for predicting the period of mosquito development on the basis of meteorological conditions is practical only if it depends on weather factors that are normally recorded at weather stations. The thermal condition of a pool is dependent largely on meteorological phenomena; but it is influenced considerably by edaphic factors as well. The probability of estimating the period of mosquito development so far as it is related to thermal conditions of the environment depends theoretically on (i) the degree to which the environment is affected by meteorological conditions and (ii) the accuracy with which the meteorological conditions can be predicted or recorded.

Edaphic factors cannot be neglected in the study of mosquito development, especially when rates of development are compared for different geographical areas. The effects of meteorological phenomena are regulated continually by subsoil temperatures to a degree that varies with elevation and geographical location. Subsoil temperature normally fluctuates from season to season. Although it fluctuates between summer and winter in permafrost areas, the daily variation during late spring and early summer is minimal and almost negligible. The quasi-constant nature of subsoil temperatures during the period of mosquito development in the study area obviated their inclusion among the variables that normally influence the thermal condition of pools.

At least four meteorological factors were considered to have measurable effects on the environment of immature mosquitoes, *i.e.*, air temperature, wind, solar radiation, and precipitation. Rainfall has been described as a limiting factor for mosquito prevalence in temperate and subtropical areas by Headlee (1929, 1930). Mosquito development in subarctic muskeg with subjacent permafrost is rarely restricted by insufficient water in breeding pools. The correlations in the Churchill area were confined therefore to three factors: air temperature, wind chill, and daily sunshine.

(I) *Air temperature.* Air temperature is recorded at weather stations with various degrees of detail. All weather offices customarily record the daily mean temperature; but the reliability of the stated mean varies according to the number of daily readings upon which it is based. For purposes of this study the maximum and minimum air temperatures were used in correlations between pool temperature and meteorological conditions. The daily averages of the maximum and minimum air temperatures were correlated with the daily average one-inch temperatures of the water in eight mosquito pools of various sizes and depths for 45 consecutive days during a normal[6] period of mosquito development. This procedure provided 360 pool temperatures for correlation with air temperature over the 45-day period. The regressions for this correlation are shown in combination with the dot chart in Figure 1. The coefficient of correlation between temperature of the pools and air temperatures was 0.872, with a probable error of ± .079.

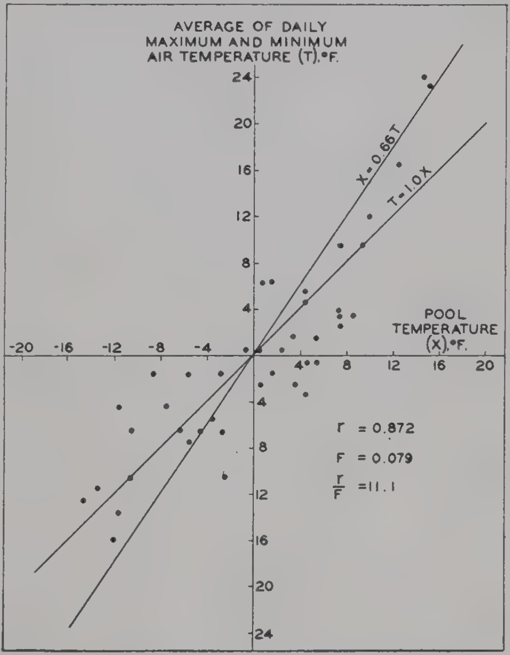

FIG. 1. The daily mean temperatures in degrees F from the seasonal means of (i) the average of the maximum and minimum daily air temperatures and (ii) pool temperature at Churchill, Manitoba, 1952. Each dot represents the average of eight daily mean temperatures, each of which was recorded from one of eight mosquito pools under observation. Coefficient of correlation = r and its probable error = F.

The coefficient of correlation was based on the relation between the average daily temperature of eight pools and the average of the daily maximum and minimum air temperatures. The possibility that the relation depends on several physical phenomena such as conduction, radiation, absorption, and convection of heat was recognized throughout the study. The comparative importance of these physical factors in the transfer of heat between the surface of the earth and the lower layers of the atmosphere is still largely unknown on a quantitative basis for biological environments. Therefore the possible influence of empirical classifications of the temperature data on the true coefficient of correlation was also considered. The effect of arbitrary manipulation of weather data on the true relation between air and pool temperatures was tested by varying the treatment of the same data on air temperatures. Three coefficients of correlation (r', r'', r''') were obtained on the basis of three classifications of air temperature over the same period as follows: (i) an average of the maximum and minimum of the current day (r'), (ii) a daily mean of the two-hourly recordings during the current day ending at midnight (r'') and (iii) an average of the daily means of two-hourly recordings during both the previous and the current day ending at mid-night (r'''). Differences between various pairs of these three coefficients of correlation were tested by the method of transforming values of r to the z distribution (Fisher 1950). The values of the coefficients and the significance of the differences between pairs of these coefficients are shown in Table I. The first of the three coefficients (0.872) with a probable error of ± 0.079) has the highest ratio of r to 6 times the probable error and indicates a more accurate treatment of the data as compared with the remaining two. Observations indicated that the lapse in pool temperature in relation to falling air temperature depended considerably on the thermal condition of the banks surrounding the pool, *i.e.*, pool temperature rose more quickly and fell less quickly on the second day of a warm, sunny period than on the first, and similarly on the third as compared with the second. The rhythmic warming and cooling of pool water with the daily rise and fall of air temperature is variable. The maximum pool temperature was reached at various times about 1500 hr in the afternoon and the minimum was reached at various times about 0200 to 0400 hr in the morning. Apparently variations in the times that pool temperature reached the maxima and minima depended on the weather conditions that increased or decreased the influence of one or more of the several physical means of heat exchange such as conduction, radiation, absorption and convection. The relation of the significance of differences between the coefficients of correlation in Table I to the environmental conditions during the study indicate the importance of selecting the proper treatment of data in preparation for statistical analysis. This is especially true when voluminous records such as weather data are condensed by empirical classification to facilitate correlation methods. The differences r'-r'' and r'''-r'' are significant at the 0.1 and the 1 per cent levels respectively. This is to be expected since the coefficient r'' is based on the mean of two-hourly recordings for each day ending arbitrarily at midnight according to standard practice in weather offices. The mean of temperatures recorded during the day and ending at midnight represents the mean air temperature for the *civil day* rather than that for the *daily oscillation* of air temperature that influences the gradual warming and cooling of pool water. This physical reasoning substantiates the high level of significance of r' on the basis of its probable error. It is probably true that the minimum air temperature for any individual day gives some measure of the thermal condition of the pool banks for the previous day and consequently approximates the daily oscillation of air temperature more closely; this may account for the approximate agreement between r' and r''' and the fact that the difference r'-r''' is not significant. The higher probable error in r''' as compared with that in r' indicates that the average of the maximum and the minimum is the most accurate classification of air temperature of the three treatments tested for influence on pool temperature. The maximum and minimum air temperatures are not only easily recorded but they are also to be preferred on the basis of their common use in weather offices.

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[6] In this paper, the term "normal" means the average for a season, weather, meteorological element, etc., on the basis of the period covered by weather records for Churchill, *i.e.*, 20 years or more.

TABLE I. Coefficients of correlation for the relation between air temperature and the average daily temperature of eight pools and the significance of intraclass differences between paired coefficients based on three classifications of the same air-temperature data.

		LEVEL OF SIGNIFICANCE OF DIFFERENCE SHOWN BY THE t VALUE FOR TRANSFORMED VALUES IN THE Z DISTRIBUTION	
Classification used for air-temperature data	Coefficient of correlation (r) with probable error in parentheses	Difference between values of Z* corresponding to r	Level of significance† of the difference on the basis of t values
Average of maximum and minimum of the current day	$r' = 0.872 (\pm 0.079)$	$Z' - Z''$ $Z' - Z'''$	$<.001$ $>.50$
Daily mean of two-hourly recordings during the current day	$r'' = 0.771 (\pm 0.087)$	$Z'' - Z'$ $Z'' - Z'''$	$<.001$ $<.01$
Average of the daily means of the previous and the current day	$r''' = 0.879 (\pm 0.091)$	$Z''' - Z'$ $Z''' - Z''$	$>.50$ $<.01$

*Coefficients of correlation r treated by the transformation $Z = \frac{1}{2} [\log_e (1+r) - \log_e (1-r)]$.

†Student's t test.

(II) *Wind chill.* Wind chill is a measurement of the cooling power of the atmosphere on the basis of wind speed and temperature. Cooling power of dry atmosphere has been described by Siple and Passel (1945), particularly at the lower temperatures. Wind chill based on dry air has been recorded continuously at the Churchill weather station in recent years in kg-cal/m^2/hr. The daily average wind chill was correlated with pool temperature for the 45-day period used for correlations of pool temperature with air temperature. The coefficient of correlation between variations in pool temperature and those in wind chill was −0.735, with a probable error of ±0.048 (Fig. 2). This coefficient is significant on the basis of the magnitude of its probable error. When the correlation between pool temperatures and wind chill was obtained for constant periods of daily sunshine, the coefficient ($r_{XZ.Y}$) dropped to −0.655, with a probable error of ±0.043.

Theoretically, the computations of wind chill used in these calculations are not exact for all conditions. The thermal conductivity of air increases with an increase in its moisture content. The average moisture content of air in the Churchill region is usually low, justifying the use of dry atmospheric cooling values for most of the year; but during late spring and early summer, when absolute humidity is somewhat higher, the values for wind chill calculated on a dry air basis are probably below the true values. As stated by Siple and Passel (1945), the computation of wind chill may also be subject to errors caused by radiation and thermal convection. From physical principles, the computation of wind chill was probably slightly low for (1) atmosphere of high moisture content, (2) high degrees of convection, and (3) low wind velocities, and by the same token was too high for completely stable and calm air conditions.

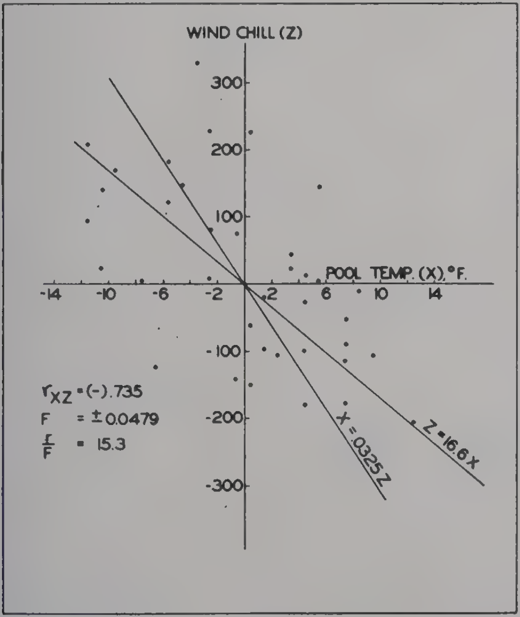

FIG. 2. The daily mean departures from the seasonal means of (i) cooling power of dry atmosphere (wind chill) in kg.-cal./m^2/hr and (ii) pool temperature in degrees F at Churchill, Manitoba, 1952. Each dot represents the daily average of eight mean temperatures, each of which was recorded from one of eight mosquito pools under observation. Coefficient of correlation = r and its probable error = F.

(III) *Solar radiation.* Solar radiation is the principal factor in the variations of temperature in different portions of even small shallow pools in the north (Haufe, to be published, a). Normally at most weather stations it has been recorded as the numbers of hours of sunshine per day. This

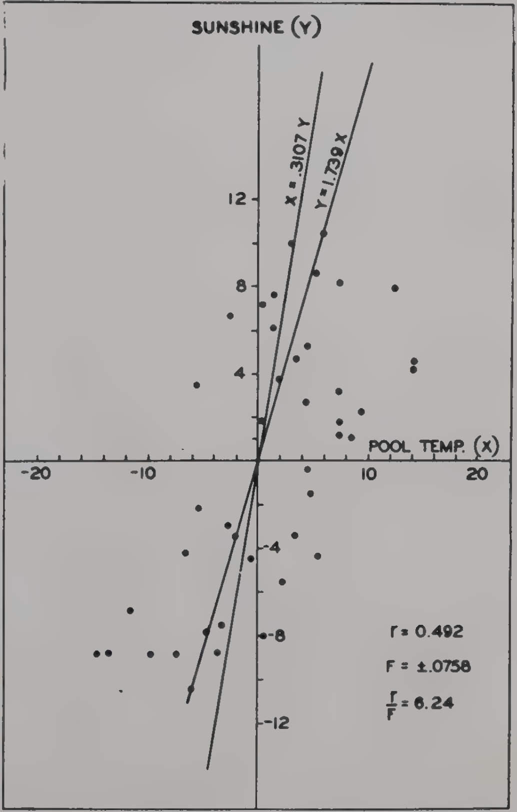

FIG. 3. The daily mean departures from the seasonal means of (i) sunshine in hours and (ii) pool temperature in degrees F at Fort Churchill, Manitoba, 1952. Each dot represents the daily average of eight daily mean temperatures, each of which was recorded from one of eight mosquito pools under observation. Coefficient of correlation = r and its probable error = F.

type of data is inadequate for a quantitative analysis of the effect of solar radiation on mosquito environment since basing solar radiation on daily periods of sunshine arbitrarily presupposes that intensity of solar radiation, and hence insolation of a pool, remains constant throughout the day. Appreciable amounts of solar radiation are detectable even on days with complete cloud cover.

Since recordings by an actinograph were not available at Fort Churchill for this particular study, the correlation was based on the usual sunshine data. The relation between the average daily pool temperatures and daily periods of sunshine for the 45-day period of study is shown in Figure 3. The coefficient between the two variables was 0.492, with a probable error of ±0.076. A value of 6.24 for the ratio of the coefficient to its probable error suggests that there is correlation under the rigorous standards required to distinguish the principal meteorological factors that influence mosquito environment. Other studies (Haufe, to be published, a) suggest that the value of the coefficient was reduced through the use of inadequately quantitative data for solar radiation.

(IV) *Other factors.* At least two factors can be cited as qualifying influences on the regulation of pool temperatures by the principal meteorological factors. Rainfall changes the pool temperature by adding water of a temperature different from that in the pool. During the passage of cold-weather fronts, falling rain may be warmer than the air temperature, and, depending on the time of season, cooler or warmer than pool temperatures. It is not possible to predict corrections for this type of condition; but approximations in temperature correction may be made after the event when the course of pool temperatures is being followed on the basis of calculations from meteorological records. This point will be more adequately discussed in a later section. Air-mass circulation also qualifies the effect of other meteorological factors as a result of certain cloud conditions which are associated usually with general patterns of circulation over a continent. Cloud conditions influence considerably the effect of solar radiation on the temperature of mosquito pools.

Relation of Pool Temperature to Meteorological Conditions

The purpose of all correlations between meteorological factors and pool temperature was to analyze the quantitative effect of a natural combination of the most influential factors such as air temperature, wind chill, and solar radiation on the temperature of environments of immature mosquitoes. The average daily thermal effect of meteorological conditions on the temperature of water in mosquito pools was computed according to a formula based on the coefficients for individual meteorological factors. The weighted average daily thermal effect of meteorological conditions (S) for any 24-hour period was based on the number of degrees by which the minimum daily air temperature exceeded 32° F (T_1), the number of degrees by which the maximum daily air temperature exceeded 32° F (T_2), the wind chill (dry cooling power of the atmosphere) in kg-cal/m²/hr (Z), and the daily amount of sunshine measured in hr (Y). The expression that fits the correlation data best is of the form

$$S = \frac{(T_1 + T_2)\ \sqrt{Y+1}}{2Z} \qquad \text{(I)}$$

where $\frac{T_1 + T_2}{2}$ represents air temperature.

This expression is based on independent reasoning from physical principles of gain and loss of heat by a body. Although the three principal environmental factors that combine to give S are reliably based on rigorous statistical tests it is also recognized that these factors are probably influenced by lesser factors that contribute to variations under natural conditions. The variability of the ratio of temperature at one inch below the surface in pools to each of the three factors air temperature, radiation, and wind chill was calculated as a prerequisite to the proper weighting of a formula. When each factor was evaluated from data of two seasons subject to influence from the remainder of the environmental conditions the coefficient of variability for this ratio was 32 per cent for air temperature, 50 per cent for wind chill and 49 per cent for solar radiation. The relation of pool temperature to air temperature is less variable since the air temperature is largely dependent on large masses of stable air. Theoretically, the temperature of the surface of the terrain and static pools should follow that of the lower layer of the air mass with varying amounts of lag depending on the influence of other factors. Radiation and wind chill may be considered to oppose each other in the modification of effects of air temperature on pools. Since the coefficients of variability are approximately equal for wind chill and radiation there is no necessity to weight them further in the expression for S. The relation between wind chill and pool temperature is rectilinear but the effect of radiation on pool temperature is curvilinear. Dulong and Petit (Stewart and Satterly 1946) made a laborious investigation of the variation of emissive power of a radiating surface in relation to the temperature of surrounding media. They expressed the relation as follows: "For a given excess of temperature the rate of cooling increases in geometrical progression as the temperature of the enclosure increases in arithmetical progression." The net gain of temperature in a pool from radiation therefore decreases for a given intensity of sunlight as the temperature of the pool rises in relation to the air temperature. For example, cold pool water warms up quickly in early morning under radiation when the temperature differential between the pool and warmer air is large; but in the afternoon the rate of warming from radiation decreases as the pool temperature approaches the air temperature and a larger proportion of heat is emitted from the pool through outgoing as compared to incoming radiation. This general relation is verified from correlation data when Y to the power ½ is used in the expression for S. For practical purposes the value of S cannot equal zero on a day when radiation in hours of sunshine is recorded as zero. If $\sqrt{Y+1}$ is used instead of $\sqrt{Y}$ the formula applies to overcast as well as sunny days.

Points showing the relation between the average daily thermal effect of meteorogical conditions (S) and the daily average of one-inch pool temperature (X) are plotted in Figure 4. The points represent 45 consecutive days in which weather was extremely variable with precipitation on all but 14 days. The circles represent days in which there was sufficient precipitation to raise the water level in the pools under study. The crosses represent days that were hazy or partially overcast with warm temperatures and exceptionally high absolute humidity. The effects of heavy precipitation and inadequate quantitative data for solar radiation are obvious.

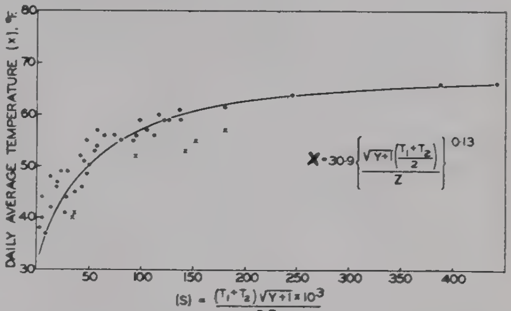

FIG. 4. The average daily thermal effect of meteorological conditions (S) and the daily average pool temperature (X) in degrees F for eight pools. Dots represent days with little or no cloudiness; crosses, the days with haze and exceptionally high absolute humidity but no rain; circles, the days with heavy overcast and sufficient precipitation to raise water levels in static pools.

The data recorded for the 14 days that had no precipitation during daylight hours and insufficient amounts during darkness to change the water levels in pools are summarized in Table II. When log X is plotted against log S for the values in Table II the relation is that of a straight line as shown by the dots in Figure 5. The equation describing the relation is therefore of the form $X = a\ S^n$. It follows then that the particular smoothed parabola may be plotted to represent the relation between X and S by subjecting most-representative pairs of points to the relation

TABLE II. Weighted average daily effects of meteorological conditions (S) on pools for 14 days not characterized by heavy overcast or precipitation

Date (1952)	Average of mean pool temp. °F (X)	Minimum daily air temp. °F	T*	Maximum daily air temp. °F	T*	Daily average wind chill kg-cal/m²/hr (Z)	Daily sunshine hr (Y)	$\frac{(T_1+T_2)\sqrt{Y+1}}{2Z}$ (S)
VI-30	66.0	57	25	84	52	330	13.0	.443
VI-29	65.5	58	26	84	52	384	13.4	.388
VI-28	64.0	46	14	79	47	422	16.7	.302
VII-7	60.0	41	9	62	30	600	14.1	.137
VI-22	59.0	40	8	55	23	537	16.9	.126
VI-23	57.0	42	10	52	20	631	17.4	.102
VI-24	56.0	40	8	52	20	526	11.5	.095
VI-20	55.0	40	8	57	25	639	13.5	.092
VI-17	53.0	32	0	58	26	618	14.9	.084
VI-19	51.0	39	7	56	24	703	4.4	.053
VI-14	48.5	35	3	53	21	719	5.9	.044
VI-12	44.0	32	0	51	19	633	16.7	.034
VI-7	42.0	40	.8	58	26	779	0.0	.021
VI-8	37.0	33	1	44	12	998	0.0	.007

*The number of degrees by which the minimum or maximum air temperature exceeded 32° F.

$$\log S - \log S_1 = \frac{\log S_2 - \log S_1}{\log X_2 - \log X_1}(\log X - \log X_1). \qquad \text{(II)}$$

Comparison of various curves with the trend of the point cloud in Figure 4 showed that the particular relation between X and S is fitted best by the parabola

$$X = 30.9 \left\{ \frac{\sqrt{Y+1}\left(\frac{T_1+T_2}{2}\right)}{Z} \right\}^{0.13} \qquad \text{(III)}$$

For practical purposes within the degree of variability experienced the formula can be simplified to the form

$$X = 31 \left\{ \frac{\sqrt{Y+1}\left(\frac{T_1+T_2}{2}\right)}{Z} \right\}^{1/8} \qquad \text{(IV)}$$

A mathematical check for the conformity of the simplified form of the equation to the point cloud is shown in Figure 5. The crosses represent values of X calculated by means of equation IV and they obviously fit the original straight line more closely than the dots.

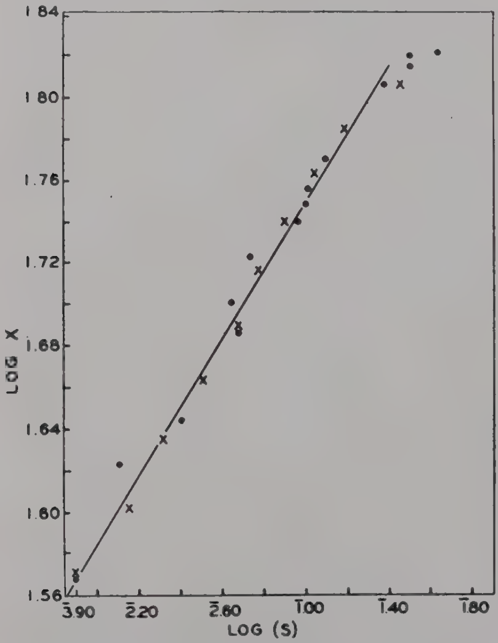

FIG. 5. Agreement of (i) values taken from field records (dots) and (ii) values based on the established equation IV (crosses) in the relation between pool temperature (X) and average daily thermal effect of meteorological conditions (S).

The discrepancies shown by the values represented by crosses and circles in Figure 4 are probably explained by the weather conditions recorded for those days. The crosses represent the comparatively few days when the general circulation was from the south to southeast. This type of circulation produced warm, humid air conditions as compared to the warm, dry air conditions associated with the more prevailing south to west circulations. The calculated daily thermal effect of meteorological conditions was undoubtedly high on those six days since the method of measurement of cooling power of the atmosphere disregarded the high rate of thermal conductivity due to the excepitonally high moisture content of the air. Haze was usually associated with south to southeasterly circulation. Quantitative recordings by an actinograph would undoubtedy show a proportionately lower rate of insolation than recordings based on hours of sunshine. This circumstance would also partially contribute to the high value of S on these days. The departure of the values represented by circles from the smoothed curve are probably associated with cloudy conditions before and after the periods of precipitation that were recorded on these days. Even with complete overcast on days when no sunshine was recorded by the usual method, spot recordings of solar radiation by a photoelectric heat radiation meter were obtained up to 0.55 g.-cal./cm^2/min. High pool temperatures also may have been partially due to the addition of precipitation that was warmer than the original pool temperature. However, consistently high pool temperatures on rainy days during the passage of both warm and cold weather fronts indicate that inadequate records of lower amounts of solar radiation were mainly responsible for the low calculated values of S.

THERMAL CONDITIONS OF ENVIRONMENT

"Time x temperature" Components

Concepts of developmental rates in life-cycles of insects have generally been described on the basis of the two parameters, time and temperature. Several thermometabolic curves have been constructed to approximate the velocity of development either for various stages or for the whole development of an organism. The views of Bodenheimer (1927), Bodine (1925), Crozier *et al.* (1926), Krogh (1914), Peairs (1927), Pearl (1927), Sanderson and Peairs (1917) and others are possibly resolved into four principal theories as to the nature of the velocity curve. Some of the viewpoints have been determined by laboratory investigations; others are the result of field investigations on various arthropods. A number of workers, notably Bodine (1925), Cook (1927), and Parker (1930), have shown that variable temperature has an accelerating effect upon insect metabolism. Developmental rates for mosquitoes may be higher under natural conditions with variable temperature than in a laboratory at comparable constant temperatures.

In earlier investigations at Fort Churchill by Hocking *et al.* (1950) the "degree-day" with an empirical lower threshold of 32° F for air temperature was suggested as a suitable "time x temperature" component to describe the period of development of northern *Aedes* mosquitoes. The detailed studies described in this paper on the biology of *Aedes* mosquitoes in the same area indicated that the lower threshold of development of individual species must also be considered when these parameters are used.

The development of *A. communis* was studied in detail during one season. The results of this investigation are tabulated in Table III. The temperatures shown are based on the average one-inch temperatures of the pools during the period of development of the mosquitoes: the one-inch pool temperatures were corrected for effectiveness on mosquito development from curves that represent the daily vertical displacement of larvae in a pool in relation to temperature gradients in the water (Haufe, to be published, a). As explained in the paper just mentioned, there is extreme variation of temperature within a pool. Mosquito larvae select temperatures both horizontally and vertically. Both displacements are important in the tabulation of pool temperatures that affect the development of mosquitoes; but only one, the vertical displacement, can be usefully employed in estimating the actual temperature that directly influences development. For instance at Fort Churchill, *A. communs* usually selects the surface layer of water until the surface temperature rises beyond 62° F. Thereafter larvae aggregate at lower levels, except for occasional sorties to the surface. *A. communis* has a temperature preferendum of approxiamtely 61° F based on field studies. This behavior pattern was incorporated in the method of estimating pool temperatures that correspond to the development of mosquitoes. The recorded average one-inch temperature of a pool was the average of half-hourly temperatures for the day taken from a continuously recording thermometer. Therefore all half-hourly temperatures above 61° F were reduced to 61° F in the calculation of daily "effective" one-inch temperatures that were related to mosquito development. The temperature to which larvae were theoretically subjected on the basis of these corrections is designated as the "effective pool temperature" in further discussion.

TABLE III. Periods of development of males and females of *A. communis* at various average "effective" environmental temperatures

Pool	MALES		FEMALES	
	"Effective" environmental temperature °F (t)	Developmental period, days (D)	"Effective" environmental temperature °F (t)	Developmental period, days (D)
A (1951).....	45.5	36	46.0	39
B (1951).....	46.7	33	46.6	36
W (1952).....	46.9	28	47.8	33
X (1952).....	47.4	24	48.5	29
V (1952).....	49.9	23	50.4	25
Y (1952).....	52.9	18	51.9	23
Z (1952).....	No emergence		53.3	20

When the period of development was plotted against the average effective pool temperature, the curve could be described as an equilateral hyperbola at least for the range of temperatures found in the area under natural conditions. The general equation of the curve representing the relation of mosquito development to parameters of time and temperature is of the form

$$D\ (t - C) = K, \qquad \text{(V)}$$

where D is the period of development, t is the average effective environmental temperature, C is the lower threshold of development for the species, and K is a thermal constant in units of "time x temperature."

The curves of development for *A. communis* under natural conditions are shown in Figure 6. The equations comparing the development of males and females indicate that the lower threshold of development for both sexes in natural

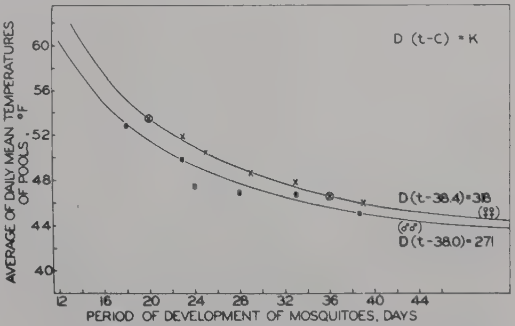

FIG. 6. Average daily mean "effective" environmental temperatures and periods of development of males (squares) and females (crosses) of *A. communis*. "Effective" environmental temperature (t) is temperature that is corrected on the basis of behavior patterns of mosquitoes in a pool and does not correspond exactly to absolute pool temperature (X) (see text).

pools was approxiamtely 38° F; but the thermal constant for females was 318 degree-days as compared to 271 for males. The lower thermal constant is a direct consequence of the three-day period by which the peak emergence of males precedes that of females. The equilateral hyperbolae in Figure 6 were drawn to satisfy two extreme values obtained for the period of development of each of the sexes, *i.e.*, those in pools A and Y for males, and those in B and Z for females as tabulated in Table III. The values from other pools were plotted on the same graph to indicate the degree of agreement between periods of development that are described by the hyperbolic relation based on the parameters time and temperature. The curves were not produced to apply to pool temperatures above 62° F since studies on the behavior of *A. communis* under natural conditions showed that the species did not select temperatures above 62° F for its environment if there were vertical or horizontal temperature gradients in the pool (Haufe, to be published, a).

Comparison of Species in Rates of Development

The periods of development of pest species of mosquitoes at Fort Churchill were compared during the summer of 1952 in at least three pools for each species. Curves describing rate of development were constructed from the two extreme values obtained for each species. The remaining value (or values), as described previously for *A. communis,* provided a check on the reliability of each specific curve. It was assumed that the equilateral hyperbola was valid in describing the development of other mosqutio species over the range of pool temperatures experienced under natural conditions. Observations of the behavior of larvae of *A. impiger, A. punctor,* and *A. nigripes* indicated that their temperature preferenda were approximately the same as that of *A. communis.* Temperature preferenda apparently were below 61° F for *A. impiger* and *A. nigripes* and below 63° F for *A. punctor.* Other species such as *A. excrucians, A. hexodontus, A. pionips, A. campestris,* and *A. flavescens* showed indications of preferring higher temperatures on occasion; therefore the one-inch temperatures, irrespective of magnitude, were considered to be the effective developmental temperatures of these species.

The hyperbolic curves constructed from data on the development of six species of *Aedes* mosquitoes are shown in Figure 7. The curves indicate that the lower thresholds of development of the larger species, *i.e. A. excrucians, A. pionips,* and *A. hexodontus,* are higher than those of the smaller species, *i.e. A. communis, A. punctor,* and *A. impiger,* The larger species except *A. hexodontus* appear to have the larger thermal constants. In studies on the behavior of adult mosquitoes (Haufe, to be published, b), populations of *A. hexodontus* usually reached their peaks more abruptly than those of any other species in the same area. The normally short period of emergence for a seasonal brood is associated with the comparatively low thermal constant for this species. This suggestion is in agreement with observations on the associations between *A. punctor* and *A. hexodontus* in field pools in the same locality in each of three successive years. Although often associated with *A. punctor* in the same pool, *A. hexodontus* was not observed to appear in the pool as early in the season as the former. However, the period between the appearances of *A. punctor* and *A. hexodontus* adults was generally shorter and was certainly never longer than that between the appearances of *A. punctor* and *A. hexodontus* larvae in the same pool.

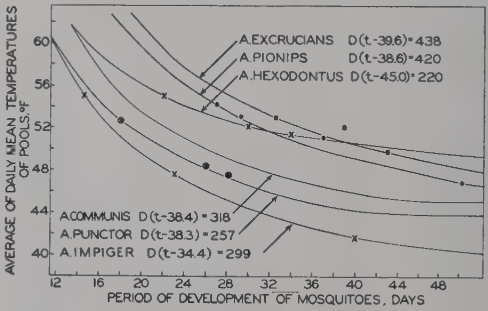

Fig. 7. Equilateral hyperbolae describing periods of development in relation to "effective" environmental temperature of the females of six common species of *Aedes* mosquitos at Fort Churchill, Manitoba.

The thermal constants and lower thresholds of development for the common species of *Aedes* at Fort Churchill are tabulated in Table IV. *A. nigripes* did not breed in the area selected for the study. Observations on open tundra indicated that this species had approximately the same lower threshold of development as *A. impiger,* but probably had a slightly higher thermal constant. *A. impiger* and *A. nigripes* larvae appeared about the same time in pools, but the adults of *A. impiger* preceded slightly those of *A. nigripes* in order of appearance in flight and attraction to man. *A. flavescens* might be expected to have a developmental curve approximating that of *A. excrucians.* These two species appeared as larvae in pools and were observed for the first time as adults on approximately the same date each season. *A. campestris* probably parallels *A. excrucians* most closely in its development. *A*

TABLE IV. Thermal constants and lower thresholds of development of *Aedes* mosquitoes at Fort Churchill, Manitoba

Species	Thermal constant (°F x days)	Lower threshold of development °F
Females		
A. impiger (Walk.) *......	300	34
A. nigripes (Zett.) *.......	300	34
A. punctor (Kirby) *......	260	38
A. communis (Deg.) †......	320	38
A. hexodontus Dyar *......	220	45
A. picnips Dyar ‡.........	420	39
A. excrucians (Walk.) *....	440	40
A. flavescens (Muller) ‡....	440⁑	40⁑
A. campestris D. & K. ‡...	320⁑	38⁑
A. cinereus Mg. ‡.........	260	38
Males		
A. communis (Deg.).......	270	38

*Posing a serious problem through abundance and intense biting.
†Causing slight or no nuisance to man.
‡In moderate numbers or exhibiting moderate biting activity, or both.
⁑By inference from field observations on order of succession of and association with the various species throughout the mosquito season for 3 consectuive seasons.

cinereus was associated with *A. punctor* in one of the pools under observation. *A. cinereus* adults emerged 1 to 2 days after *A. punctor* and the species probably have nearly similar thermal constants.

Relation of Topography to Development

The topography of some areas probably influences the development of mosquitoes to considerable degres depending on the effect of physiographical features on the climate. Mosquito development was delayed very little in large deep pools as compared to small shallow pools. The studies on behavior of immature mosquitoes had shown that larval activity was restricted usually to warm, shallow peripheral portions of pools larger than normal. For this reason it is probable that mosquitoes that develop in large pools are subject to effective environmental temperatures that closely approximate those of smaller pools.

In the level muskeg common to terrain in the Fort Churchil alrea (Fig. 8) topographical features had little effect on the uniformity of emergence of mosquito populations except where large snow drifts covered pools late in the season. Significant variations in emergence of adult populations were associated with greater density of shrub and particularly of forest cover. Observations on populations with mixed species indicated that the time from beginning to end of mosquito emergence was 4 to 5 days in tundra pools as compared to 6 to 10 days in woodland pools. Observations on populations containing a single species, *A. communis,* showed that the time from the beginning to the end of emergence of the adult females was approximately 4 to 5 days in pools exposed completely to the free play of meteorological elements, 5 to 6 days in pools surrounded by low shrub, and 8 to 10 days in pools closely bordered by spruce trees. The periods for the complete emergence of both sexes were 2 to 4 days longer in each category because the emergence of males preceded that of females by approximately that period under natural conditions. In large pools with highly irregular contours, vegetative cover along the banks may interfere with the effects of meteorological elements on the pools so that complex patterns of behavior may develop within a population of mosquitoes. The influence of environmental factors may be so complex that a population of a single species is divided into groups isolated from each other by unfavorable environmental conditions throughout most or all of their period of development. A general survey in 1950 within the transition belt between forest and tundra was designed to give approximate figures on the variation of emergence in different localities. A large number of pools were sampled systematically at daily intervals to recover fourth instar larvae of *A. communis.* The pools represented a series on level mossy plain progressing from the shallow, regular-bordered, barren type of pool to the irregular-bordered, deep type found in small stands of scrub spruce. Six pools were sampled at each station and fourteen stations were included in the series between the two extremes of vegetative cover. The variation of the time marking the last capture of fourth instar larvae was 3 to 5 days or almost 20 per cent of the average period of development at each station for pools on barren plain as compared with 6 to 10 days or 41 per cent of the developmental period at each station within stands of scrub spruce. Assuming that these variations in rate of development of larvae are reflected in the variations of periods of emergence of adults, the abundance of adults is less predictable in wooded areas with irregular pool conditions than in the tundra. Mosquitoes apparently select specific breeding places (Haufe 1952; Horsfall and Morris 1952). This tendency may eliminate much of the variation in rate of development of mosquitoes caused by topographical influences that are associated with various types of vegetative growth.

Variation of Temperature between Pools

The accuracy of formulae suggested for the prediction of mosquito emregence depends largely on the degree of variation in temperature to be expected between pools. We stated above that pools selected for correlations represented a wide varia-

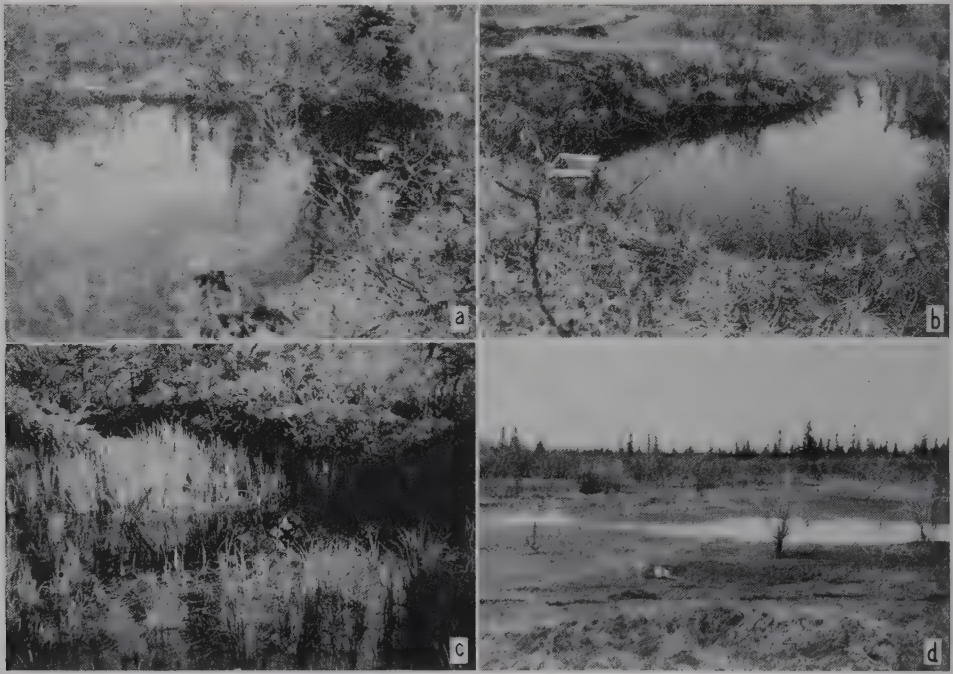

Fig. 8. Pools typical of the study area, in transition between tundra and Boreal forest. a and b, Deep, permanent type with steep banks in scrub-willow muskeg. c, Quasi-permanent, grassy type of shallow pool in scrub-spruce forest. d, Shallow, flood-plain type near water course with muck bottom.

tion in size and in proximity to vegetative cover. A comparison of mean daily temperatures at a depth of one inch is presented in Table V for six pools. The pools listed in the table were classified as follows: *V*, *W* and *X* were small, average and large pools respectively with no vegetative cover to influence the effects of either solar radiation or wind. *X*, *Z*, and *X-1* were all averaged-sized pools; but their vegetative cover was characterized by tall grass, scrub willows and scrub spruce respectively. The last-mentioned pool represented a very small proportion of the pools usually found in tundra or tundra-forest transition. It was also the last pool to show open water in the spring since it was beneath a large snow drift in a small island of scrub spruce. The period shown in the table, June 11 to July 2, 1952, does not represent the periods of development of mosquitoes in respective pools but rather the period beginning with the disappearance of surface ice from *X-1* and the drying up of *V*. The emergence of mosquitoes was almost completed in pool *V* by the time water disappeared. The six pools were selected at intervals of approximately a week as open water appeared. They were primarily designed to provide a series of "time-temperature" products in rela-

Table V. Variation of mean surface temperatures among pools representing a wide range of size and vegetative cover at Fort Churchill, Manitoba, in 1952

Date	Mean Pool Temperature (°F)						Maximum deviation
	V	*W*	*X*	*Y*	*Z*	*X-1*	
June 11....	46.0	46.5	46.0	45.5	49.0	46.0	±2.5
12....	49.2	48.5	47.5	45.5	46.0	47.0	±2.2
13....	47.6	48.0	47.0	46.0	46.5	46.0	±1.2
14....	52.0	50.0	50.0	49.0	48.5	48.0	±2.4
15....	49.2	50.0	49.0	48.5	49.0	47.0	±1.8
16....	51.2	50.5	50.5	50.5	50.0	50.5	±0.6
17....	53.5	54.0	53.0	53.5	51.5	52.5	±1.5
18....	56.5	58.5	57.0	56.7	56.5	57.0	±1.2
19....	54.7*	50.5	50.0	51.5	49.0	48.5	±4.0
20....	55.2	54.5	54.5	54.0	55.5	54.5	±0.8
21....	61.2	60.5	60.0	58.5	61.5	59.5	±1.7
22....	62.0	60.0	60.2	59.0	61.0	58.5	±1.9
23....	58.0	59.5	58.0	57.0	59.0	57.0	±1.4
24....	58.0	59.0	58.5	57.5	58.0	57.5	±0.9
25....	54.7	56.0	54.5	53.5	55.0	52.5	±1.9
26....	56.0	57.5	56.0	57.5	56.0	54.0	±2.2
27....	63.0	62.0	60.5	61.0	62.0	57.0	±3.9
28....	66.0	65.0	63.0	65.0	65.0	59.0	±4.8
29....	65.5	69.0	65.0	69.0	68.0	62.0	±4.4
30....	68.0	69.0	68.5	70.0	69.0	63.5	±4.3
July 1....	61.2	62.0	60.5	63.5*	59.5	57.0	±3.5
2....	50.0	51.5	50.5	49.5	49.5	49.5	±1.4
Average..	56.3	56.4	55.4	55.5	55.7	53.9	.....

*Pool flooded with surface drainage following heavy precipitation.

tion to mosquito development. Consequently the series of temperatures for pools *V*, *W*, *X* and *Y* represent the environment for the later part of mosquito development while pools *Z* and *X-1* represent a period midway in mosquito development. The variation in temperatures among these pools is perhaps greater therefore than in a random selection of pools showing open water at the time of a general spring thaw. As shown in Table V, the difference in the averages of the temperatures for pools over the period are not significant on a field scale except for pool *X-1* which was specially selected for late development of mosquitoes. The maximum deviation between pools for given days varied between ± 0.6 and ± 4.8°F. Inspection of the deviations shows that they increase as the pool temperatures rise. Behavior studies on *A. communis* (Haufe, to be published, a) have shown that mosquitoes select preferred temperatures along horizontal and vertical temperature gradients and that the preferenda are at approximately 60-62° F. Since the greater deviations of temperature between pools occur above 60° F they are relatively insignificant in affecting the development of mosquitoes that are subjected to the steep temperature gradients that are characteristic of pools at northern latitudes.

DISCUSSION

Prediction of mosquito emergence depends largely on the accuracy of meteorological probabilities. Long-range forecasts show slight promise until appropriate methods have been perfected. Short-range prediction of specific mosquito emergence in northern Canada, however, may be feasible where daily meteorological records representative of the immediate area are available. The thermal effect of meteorological conditions can be additively compiled from day to day to indicate from established thermometabolic curves the expected time of appearance for a given species. The accuracy of this type of prediction would increase progressively day by day from the time of the general appearance of open water at the banks of mosquito pools to the date of general emergence of the adult mosquitoes. Judgment would be required only in the selection of the date that represents the time of general exposure of the banks of pools during the spring thaws.

Blunck (1923) suggested that the equilateral hyperbola might be adapted to describe the development of dry-land insects during the immature stages. Our studies indicate that the equilateral hyperbola is representative of the development of the post-hatching stages of *A. communis* over the range of temperatures normally experienced in pools in permafrost terrain. The use of hyperbolae to describe development under natural conditions requires that the "effective" environmental temperature based on patterns of behavior is a parameter of the "time x temperature" component for any individual species. Although the curves of development for species other than *A. communis* are based on less detailed data than those for *A. communis*, the values obtained for thermal constants and lower thresholds of development agree with the natural succession of species observed during three successive seasons. Values for developments of the various species agreed not only with the natural order of appearance of first-instar larvae in the pools but also with the peak activities of the adults.

The three-year period of study was representative of the extreme variations in meteorological conditions that might normally be expected in the area. The spring season of 1950 was exceptionally cold with monthly mean temperatures as much as 8° F below normal and precipitation above normal. The following year was a normal season for both temperature and rainfall. In 1952 monthly mean temperatures were considerably above normal through March, April, May, and June, and reached a peak of 12° F above normal in May; precipitation in these four months was the heaviest for the three years.

The algebraic expression suggested for the relation between pool temperature and meteorological factors were developed from data for permafrost terrain. Since the effects of permafrost in cooling pool water below air temperatures were quasi-stable during the periods of study and consequently were not expressed in absolute units in the derived equations, the parabolic relation (formula IV) may be restricted to typical permafrost areas. Application of this type of formula to temperate areas would require further research on the relation of seasonal variation in subsoil temperature to the effects of meteorological factors on pool temperature. As compared to permafrost areas, in which the subsoil temperature at a 6-inch depth may remain quasi-constant during late spring and early summer, in temperate climates a gradual seasonal variation is known to exist at the same depth. At lower latitudes variable subsoil temperatures may have a considerable effect on pool temperatures.

Topographical variations would undoubtedly have serious effects on the relation between pool temperatures and meteorological conditions. The Churchill area is flat; except for interference by vegetation, pools were equally and normally exposed to the natural daily succession of meteorological phenomena. In rolling, sloping, or mountainous terrain, pools may be more or less exposed to meteorological conditions characteristic of one part of the day than to those of another part, depending on the disposition of physiographical features. For instance, solar radiation, winds, cloud cover, and precipitation are all seriously influenced by mountain ranges. Schubert (1928) has described in detail the variations in the sum-effects of daily solar radiation associated with various degrees of inclination of insolated surfaces to the path of incident radiation in the region of Potsdam, Germany. From Schubert's data the effects of solar radiation on environmental temperatures in mountainous regions may be expected to be complex. Schade (1917) found that the surface characteristics of treeless terrain varied so much that extreme differences in temperature were recorded within distances as little as 50 metres on ground surfaces exposed to the weather. His detailed records showed that the difference between minima seldom exceeds 2° C; but by day, when incoming radiation is effective, the differences in maxima may be as great as 37° C for two sites at the same distance. Comparison of the effects of meteorological conditions on environments in different geographical regions would require a classification of terrain on the basis of meteorological changes that are associated with certain categories of physiographical features.

These studies indicate the necessity of continuous records as opposed to spot recordings of meteorological elements in ecological studies on mosquitoes. Ecological formulae of the type described in this paper require improvements in the general documentation of weather at meteorological stations. Three improvements that appear to be most important at the present stage of this study are: (i) records of the cooling power of the atmosphere, including thermal conductivity of air, *i.e.,* atmospheric cooling based on moisture content of the air as well wind speed and temperature, (ii) continuous summation of daily solar radiation in absolute units (g-cal/cm^2/min), (iii) more precise values of average wind speeds. In the analysis of the thermal effects of meteorological elements on mosquito pools it was remarkable to find a lower statistical correlation for daily sunshine than for average daily wind chill. It is possible that the inadequacy of the summation of solar radiation on the basis of daily hours of sunshine, as opposed to continuous recordings by actinograph in absolute units, is responsible for this relation in the data. Geiger (1941) has stressed the importance of solar radiation recorded as a daily sum in cal/cm^2 in the analysis of ecological relationships involving micrometeorological elements. This view is supported by the fact that during the studies at Fort Churchill spot recordings of solar radiation of up to 0.55 g-cal/cm^2/min were obtained with a photoelectric heat radiation meter on overcast days on which zero hours of sunshine were recorded.

In addition to its influence on environmental temperatures, solar radiation had significant effects on the patterns of behavior of mosquito larvae (Haufe, to be published, a). The sum effect of solar radiation in promoting the development of mosquito larvae in field pools may still be underestimated. Related field studies on behavior and ecology of mosquitoes (Haufe, to be published, b) have indicated that insects may develop at different rates because they behave differently in nature and that ignorance of this fact may lead to serious error.

When lower thresholds of development were used as a basis for the establishment of thermometabolic curves for mosquitoes under natural conditions, the thermal constants appeared to bear some relation to the size of the insect. The larger species generally had the larger thermal constants. Bodine (1925), Cook (1927), Parker (1930), and others have shown in laboratory experiments that fluctuating temperatures promote higher velocities of development than constant temperatures. The association between body size and thermal constant probably depends on the rate of heating and cooling associated with the ratio of surface area to the volume of the insect. Since the ratio of surface area to unit volume is greater for smaller bodies than for larger bodies, higher rates of heating and cooling should theoretically be associated with the smaller mosquitoes. Where thermal conductivity is limited to water, the greater rate of heat gain of small larvae during rising temperatures should be cancelled approximately by the greater rate of heat loss of small larvae during falling temperature. However, it is probable that mosquito larvae, especially when resting near the surface, absorb some solar radiation directly to increase their body temperatures. The behavior patterns of mosquito larvae under natural conditions during periods of high insolation indicate that this may be true, especially when environmental temperatures are below the preferendum (Haufe, to be published, a). When pool characteristics are such that the larvae can select continually temperatures that do not exceed their preferendum, the relation of surface area to body volume would be an important factor in the ability of larvae to increase body temperature by direct absorption of heat from both solar radiation and pool water.

Some important limitations to the use of the equilateral hyperbola in describing the development of mosquitoes under natural conditions must be recognized. The curve can be expected to be representative of development only over the range of temperatures below or equal to the species preferendum unless the mosquito has freedom to select temperatures that do not exceed its preferendum during the period of development. Usually the development of insects decelerates when the temperature is increased beyond the optimum (*e.g.*, Andersen 1930; Krogh 1914; Larsen and Thomsen 1940). For supraoptimum temperatures the relation between period of development and temperature would depart from the form $D(t-C) = K$. In pools studied in permafrost areas, vertical or horizontal gradients were always sufficient to permit larvae to select optimum and suboptimum temperatures during the period of development. When surface temperatures became exceptionally high in the shallow muddy pools in floodwater muskeg, mosquito larvae were commonly observed to be resting within the loose muck which formed the bottoms of such pools to a depth of several inches above permafrost in the summer. Gradients measured in pools under these circumstances had surface temperatures as high as 80° F, which was considerably in excess of the 61-63° F preferenda of some of the local species. The temperature just below the surface of bottom muck was not observed on any occasion to exceed 58° F in the smallest of pools that had water to a depth of at least two inches. Therefore it is probable that mosquito larvae in permafrost areas develop within environments that rarely, if ever, exceed the temperature preferendum. In temperate and tropical areas this is not likely to be true. The use of equilateral hyperbolae in prediction of mosquito emergence is restricted, therefore, not by geographical areas but rather by the relation of the temperature preferendum of the species to the normal climate. On the North American continent the suggested formulae may be applicable with increasing accuracy progressing north and east of the middle of the geographic distribution of a species and with decreasing accuracy progressing south and west, provided comparisons are made at equal altitudes. In mountainous terrain the same type of formulae would be more representative of development at altitudes above the mean for the vertical distribution of the species where development is subjected to suboptium mean environmental temperatures; at altitudes below the mean for the vertical distribution of a species the development would be subject to supraoptimum mean temperatures unless the character of the pools permitted selection of environments with optium or suboptimum temperatures. These conditions seriously restrict the use of the equilateral hyperbola. Much investigation appears to be necessary to establish the territorial applicability of methods discussed in this paper.

The application of physical formulae to the prediction of mosquito development may be subject to important influences from edaphic and nutritional conditions and population densities. On a local basis these influences may be expected to cause considerable variation in times of emergence by affecting the microenvironment of the immature stages. It is probable that the physical conditions of an environment such as temperature and light are limiting factors in some of the biological processes involved in mosquito development. The ecological aspects of the influence of population density, nutrition, and edaphic factors have been given little, if any, attention in investigations of mosquito biology. Beckel (1953) reported indications in preliminary experiments that temperature may be a limiting factor in the action of a hatching stimulus from decaying organic matter for some of the *Aedes* species of the Churchill area. He found that infusions of decaying mosquito bodies stimulated hatching of the eggs of *A. hexodontus* and *A. campestris* at appropriate temperatures. It is possible that the activity of microorganisms may influence the rate of hatch, especially in species that have a diapause, and thereby contribute to the variation in the developmental period in relation to physical conditions of the environment. Beckel stated that *A. hexodontus* hatched in the laboratory at temperatures slightly above 0° C. In the investigations reported in this paper the lower threshold of development was indicated to be approximately 45° F in nature for the same species. It is noteworthy that the curve did not conform with those of other species with comparable body sizes. Development may have been retarded disproportionately in the lower part as compared to the higher part of the temperature range. This would account for an abnormally high value for the apparent lower threshold of development. If other edaphic hatching stimuli are more vital to the embryonic development of *A. hexodontus* than to co-existent species the lack of these stimuli in the early flood conditions of pools might abnormally retard the general hatching of the eggs. This may cause a serious variation in lower thresholds of development that are calculated from natural emergence. Comparison of times of development and their variation in this paper are confined principally to the black-legged *Aedes* group of mosquitoes that have a diapause that is followed by a single annual brood. Generally speaking from studies on other insects the variations in rate of development are compressed in populations of single-brooded species after a diapause in the egg stage. The black-legged species of *Aedes* that form the greater part of the abundance of mosquitoes at Churchill hatch quickly in the early part of the spring with the first appearance of open water. Moisture is not a limiting factor in the development of the early species of mosquitoes in the transition area between tundra and forest; it is reasonable to expect therefore that the large variations of emergence from irregular pools is a reflection of factors influencing the development of the larval and pupal stages rather than of variation in the egg laying periods of the previous year. Preliminary laboratory experiments (unpublished) with *Aedes aegypti* have indicated that the high density of larvae commonly observed in the Canadian Subarctic may be associated with variations in the rate of development within single pools.

The phenomenon of photoperiodism should be mentioned in relation to variations in development since it has already been described for *Aedes* mosquitoes (Baker 1935; Love and Whelchel 1955). Winter larvae of *A. triseriatus* Say that are inhibited in their development under natural conditions will pupate normally if the photoperiod is artificially extended. Love and Whelchel showed that photoperiodism did not affect the hatching of ova. The unexplainable inhibition of development of *A. hexodontus* in the early stages as compared with other associated species indicates the possible influence of photoperiodism on biological grounds. From a meteorological point of view however this is less likely. The daily rate of increase in the period of daylight decreases from approximately one per cent in April to less than 0.1 per cent throughout June at Fort Churchill. Since the development of *A. hexodontus* in the Subarctic is usually confined to the month of June, the immature stages would have to be sensitive to very small changes in photoperiod to cause any signficant variation in time of pupation under natural conditions.

SUMMARY

1. Formulae for predicting mosquito emergence are suggested from three years' field observations on the development of *Aedes* species of mosquitoes at Fort Churchill, Manitoba.

2. The development of post-hatching stages of both males and females of *A. communis* could be described by a common mathematical curve provided that the immature stages were not subjected to temperatures above the optimum of the species.

3. Curves of development were drawn for the pest species at Churchill on the basis of emergences of each species in at least three pools having different thermal characteristics. Lower thresholds of development and products of time and temperature are tabulated for the periods of development of common species.

4. The tundra species of mosquito (*A. impiger* and *A. nigripes*) had lower thresholds of development approximating 34° F; the forest species (*A. communis, A. punctor, A. excrucians*) had a range of 38-40° F, except *A. hexodontus,* which appeared to have an exceptionally high value of 45° F.

5. The products of time and temperature for the period of development of both tundra and forest species where lower for the smaller than for the larger species. For the Fort Churchill area they were 260 to 440 degree-days for the common species of *Aedes*.

6. The peak emergence of *A. communis* males consistently preceded that of the females.

7. Mathematical descriptions were constructed for the relation between meteorological elements (temperature, dry cooling power of the atmosphere, and daily amount of sunshine) and the daily average of temperature of mosquito pools.

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THE FOOD OF SOME COLUBRID SNAKES FROM FORT BENNING, GEORGIA

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The food of colubrid snakes of the southeastern United States is not well known. While many accounts have appeared on snake dietary from this region, these usually are of a fragmentary nature, and generally have been incidental to taxonomic studies, annotated lists, or the like.

The Fort Benning Military Reservation is located in Chattahoochee and Muscogee counties, Georgia. The western boundary of the reservation touches the Georgia-Alabama State line. The principal area of study and collecting encompasses a 90 acre tract in Chattahoochee County (Long. 84′ 52″, lat. 32′ 25″), the so-called Magazine Area, just north of the old hospital grounds. The area is one of gently rolling hills with elevations of from 250 to 500 feet. Extensive stands of timber cover the greater part of the reservation. Prominent trees are the oaks, (white, water, post, red, and black), short-leaf pine, gum (*Nyssa*), magnolia and willow. Wild plum, holly, and small dogwoods are abundant in small patches of the larger open fields. The underbrush consists of blackberry and laurel. Vines include honeysuckle, wild grape and Kudzu (*Pueraria*). The larger open tracts (of ten or more acres) have a sparse cover of Bermuda grass. The soil is primarily sand or a friable sandy loam.

The climate is mild, allowing a long growing period. Frequent temperatures in the seventies during December and January occasionally draw snakes and lizards from their winter quarters. Some monthly temperatures (daily maximum and minimum readings) are available for 1951 and 1952. These are listed below.

Month	*Average for Month*	*Maximum*	*Minimum*
September, 1951	78.60	101.3	60.1
October, 1951	69.2	98.4	39.2
November, 1951	51.1	82.0	26.4
December, 1951	53.2	80.1	19.0
January, 1952	67.04	81.4	23.6
February, 1952	63.64	79.1	30.0
March, 1952	69.55	84.3	35.1
April, 1952	76.61	87.0	34.9

In the present study, the percentage and volume of food is recorded. Often a snake contained two or more food items. We are aware that secondary food organisms, notably insects, may appear in the stomach or the intestine of snakes that had eaten lizards, amphibians or even birds and mammals. Since most of the vertebrates eaten were little digested and their viscera unexposed, we may discount the presence of secondary food organisms in virtualy all of the snakes examined.

One of the astonishing results of this study is the high incidence of snakes containing recognizable food. In a study of New York garter snakes (*Thamnophis sirtalis sirtalis*) 382 snakes were examined. Of these, 63.1 per cent contained food (Hamilton 1951). Food occurs even less frequently in other New York snakes. Uhler *et al.* (1939) examined 893 Virginia snakes of 18 species, of which 418 individuals (46.8 per cent) contained sufficient food for analyses. In the present study, 437 snakes including 70 crotalids, were examined, of which 84.9 per cent contained food. This high proportion of snakes with food may be attributed, in part, to the great abundance of lizards and other prey species in the area studied.

Pollack made the collections and field notes. Collecting was conducted in every month, from September 1949 to May 1952. Some highway kills contribute to the collection, although most of the snakes were removed from under cover of munition boxes or taken from brushy tracts. The date of capture was recorded on tags attached to the body, several slits were made in the body and the specimens preserved in 10 per cent formalin. Hamilton examined the preserved specimens for food, reproduction and made the determinations.

Literature relating to the food of the snakes from southeastern United States is notable only for its paucity. We include important references to eastern snakes, when the species is included in our report. Surface (1906) provided the pioneer study of snake foods on our eastern snakes. Wright and Bishop (1915) include notes on the food of many snakes from the Okefinokee Swamp of southeastern Georgia. Uhler *et al.* (1939) made a detailed study of snake foods from the George Washington National Forest, Virginia. A good summary of snake foods has been provided by Schmidt and Davis (1941), generalizing on the food of those species treated in the present study. Hamilton and Pollack (1955) reported on the food of Fort Benning crotalids. We follow the arrangement and nomenclature of Schmidt (1953).

STRIPED WATER SNAKE, *Natrix rigida* SAY

Two specimens, both taken in May, 1951. A highway victim, 345 mm long, contained no food. A slightly smaller snake contained remains of a narrow-mouthed toad, *Microhyla carolinensis*.

RED-BELLIED WATER SNAKE, *Natrix erythrogaster erythrogaster* FORSTER

Seven specimens, ranging in total length from 741 to 1482 mm were taken. Four contained food. Three had eaten ranids, while a single one had fed on a large *Bufo terrestris*. A large cottonmouth, *Ancistrodon piscivorous*, had eaten a three foot red-belly, which in turn produced a large frog from its stomach.

BANDED WATER SNAKE, *Natrix sipedon fasciata* LINNAEUS

Five specimens are available for study. These range in total length from 664 to 920 mm. The paucity of water snakes in our collections is no indication of *Natrix* scarcity, for they are abundant on the reservation. Many were taken alive, some being sent to William and Lester Piper of Bonita Springs, Florida. Three snakes contained food; one had eaten a *Rana clamitans*, another an undetermined ranid, while the third contained a small centrarchid fish.

Brown Water Snake,

Natrix taxispilota Holbrook

A male with a total length of 1205 mm, taken on April 26, 1950, contained large ctenoid fish scales in the hind gut.

Wrights' Brown Snake,

Storeria dekayi wrightorum Trapido

Some of the snakes were taken in Phenix City, Alabama, a mile from the principal site of the collections. A few were recovered under loose grass and hay placed specifically to attract the snakes. An examination of 26 individuals, ranging in size from 117 to 301 mm, indicates earthworms and slugs as the principal dietary of this snake. An individaul taken on December 9, 1951 contained two small earthworms. Of the 18 snakes containing food, 14 had eaten earthworms and four had consumed slugs. A large (289 mm) snake collected on March 12, 1950 contained sand and a quantity of Collembola (30 or more). Presumably the springtails were ingested with other food or taken inadvertently.

Red-bellied Snake,

Storeria occipitomaculata occipitomaculata Storer

This is not a common snake in the area. In the northern areas where we have collected *Storeria*, the red-bellies are as common as DeKay's snake. Eight individuals were taken, ranging in size from 164 to 214 mm. Six contained food; five had eaten slugs while one had eaten an earthworm. The usual food of the red-bellied snake appears to be slugs and earthworms. It may be considered a specific feeder of these two items.

Ribbon Snake,

Thamnophis sauritus sauritus Linnaeus

The single specimen taken on June 27, 1951, with a length of 571 mm contained a large lycosid spider. No indication of other food occurred in the intestinal tract. We presume the spider to be an original food. Ribbon snakes commonly feed on earthworms.

Eastern Garter Snake,

Thamnophis sirtalis sirtalis Linnaeus

The garter snake is an uncommon species at Fort Benning. Three were collected in as many years of collecting. All contained earthworms, a common food taken by the garter snake throughout its range.

Ground Snake,

Haldea valeriae Baird and Girard

Three specimens, in size from 174 mm to 254 mm were taken on July 25 and October 13, 1950. The fat on the viscera of the October specimen was notable. One contained remains of earthworms. All had sizeable quantities of sand in the hind gut, presumably the residue from earthworms.

Hog-Nosed Snake,

Heterodon platyrhinos platyrhinos Latreille

Most writers credit this species as a key predator of toads and frogs, although its food is scarcely limited to these amphibians, as Ditmars (1933) implies. Surface (1906) examined 27 Pennsylvania specimens, recovering toads from ten individuals. Insects, some undoubtedly from ingested toads, included grasshoppers, pentatomids, cicadas and lepidopterous larvae. Single specimens contained a salamander, tadpole and a bird. Wright and Bishop (1915) record four Georgia specimens with toads, one having eaten three individuals. Beetles and grasshoppers had been eaten by five additional snakes. Uhler *et al.* (1939) recovered food from ten of 27 Virginia specimens. Four individuals had eaten toads, while three had taken frogs. Other foods include a chipmunk, mouse, and salamanders. Carr (1940) "once watched a *contortrix* (*platyrhinos*) eat five adult *Bufo terrestris*."

We have examined 42 specimens, of which 33 contained food in sufficient quantity to record. Many individuals, particularly small specimens, have the intestine, especially the hind gut, filled with sand. The present study substantiates other reports that the hog-nosed snake feeds on toads. The food is recorded in Table I. Individuals

Table I. Food of 33 *Heterodon platyrhinos platyrhinos*

Food	Per cent of Occurrence		Per cent Volume	
Insects (16)		48.5		43.8
Lepidoptera larvae	27.3		24.1	
Coleoptera	12.1		9.5	
Orthoptera	6.1		4.1	
Undetermined	6.1		6.1	
Amphibia (7)		21.2		20.9
Bufo terrestris	12.1		12.1	
Scaphiophus	3.0		3.0	
Rana	3.0		3.0	
Eurycea	3.0		3.0	
Molluscs (5)		15.1		10.9
Lizards (4)		12.1		8.6
Lygosoma	3.0		2.4	
Cnemidophorus	3.0		.2	
Lizard eggs (Ophisaurus?)	3.0		3.0	
Undetermined	3.0		3.0	
Crustacea (2)		6.1		5.5
Turtle (1)		3.0		3.0
Centipede (1)		3.0		3.0
Earthworm (1)		3.0		3.0
Spider (1)		3.0		1.2

containing food ranged in total length from 174 to 977 mm. They were collected from April 27 to November 20.

Insects are included in the tabulations only when it was considered that these items were not of secondary origin. With one exception, none of the lizards had undergone sufficient digestion to expose an insect which may have been eaten by them. The insects eaten by this snake include small, smooth-skinned lepidopterous larvae, undetermined beetles, the orthopteran *Scudderia,* and a mole cricket, *Gryllotalpa.* The amphibians were principally *Bufo terrestris,* one large (890 mm) snake containing three of these toads. Another had eaten a large *Eurycea bislineata cirrigera.* Molluscs include snails of the genus *Triodopsis.* Six large snails were recovered from the stomach of a medium-sized specimen. In spite of their great abundance, lizards do not appear to play an important role in the dietary of the hog-nosed snakes. Crustaceans include the isopod *Armadillidium,* which had been eaten in some numbers by two small snakes. One 647-mm snake had devoured a recently hatched mud turtle, *Kinosternum subrubrum.* A large scolopendrid centipede equalled a third the length of the juvenile snake that had eaten it.

SOUTHERN RING-NECKED SNAKE,

Diadophis punctatus punctatus LINNAEUS

This is a common species over the entire post. The choice hibernating site appears to be rotted logs, where, in company with *Eumeces* and salamanders of several species, it finds a winter haven. This ring-neck was rather difficult to find during the active season of other snakes. A series of six ring-necked snakes removed from a punky pine log in January 1950 had no food in the stomach or viscera. On January 31, 1951 two adults (218-236 mm) and four young (114-155 mm) were taken from a well rotted pine log. One of the adults contained several ants and a quantity of sand in the rectum. Temperature at the time of capture was 64° F.

A male (261 mm) taken in August, 1949 contained a *Lygosoma.* A ring-neck taken on May 15, 1950, had eaten a large worm. While in the winter quarters, some do feed. A male (276 mm), taken from a punky log on February 5, 1951, contained two slimy salamanders, *Plethodon glutinosus.* Two other ring-necked snakes at the same site contained no food, other than sand in the hind gut. Barbour (1950) recovered food from 18 of 53 Kentucky ring-necks. The principal food was salamanders, including *Plethodon glutinosus, Desmognathus, Eurycea bislineata* and the eggs of *Aneides aeneus.*

WORM SNAKE,

Carphophis amoenus amoenus SAY

Four specimens ranging in length from 193 to 496 mm were examined. Two contained earthworms. In the hind gut of another, sand granules were present. The largest specimen was plowed up in sandy soil on April 25, 1951, at an estimated depth of 8-9 inches. It had recently shed the skin.

EASTERN MUD SNAKE,

Farancia abacura abacura HOLBROOK

The two specimens were taken on May 2, 1951 and July, 1950. Stomachs empty, quantity of sand in the hind gut and a trace of ranid metacarpals in the hind gut of the largest. The snakes measured 702 and 768 mm respectively.

BLACK SNAKE,

Coluber constrictor constrictor LINNAEUS

The general diet of the black snake, as reported by many writers, is a varied one. Assorted vertebrates and an occasional insect provide sustenance for this widespread species. In the north, mammals apppear to predominate as food, while southern individuals fare to a large extent on lizards. This species is not a constrictor.

In stomach analyses of Pennsylvania specimens, Surface (1906) provides a diagram detailing the food of this species. Presumably the incidence of occurrence is indicated; no mention is made of the number examined. Surface includes insects, field mice, snakes, unidentified mammals, birds and their eggs, frogs, and rabbits, in such order, that make up the principal dietary of black snakes. He includes many references to other foods of the species. Wright and Bishop (1915) record as food of this species the lizards *Cnemidophorus* and *Lygosoma,* while *Bufo terrestris, Hyla carolinensis* and *H. femoralis* are included in the dietary of Georgia specimens. They include insects, beetles being the principal group taken. Ortenburger (1928) examined 22 stomachs, finding insects in all but one individual. Uhler *et al.* (1939) examined 34 Virginia blacksnakes. Of these, only 16 specimens had sufficient food to provide data useful in percentage compilations. Small mammals, snakes, birds, and insects were the principal food items.

Of the 62 Benning specimens examined, 57 (90%) contained food, a surprisingly high incidence. Less than half of the Virginia specimens examined by Uhler *et al.* contained recognizable food. Nearly two-thirds of the specimens we examined contained lizards, a reflection of the abundance of these saurians in the area studied. The smallest black snake, a recently hatched individual measuring 269 mm, contained juvenile *Peromyscus,* while the three largest (1300 mm, 1332 mm, and 1347 mm, respectively) all contained frogs. Many of the lizards and snakes were swallowed tail first. Specimens containing food were taken from February 16 to October 31 (Table II). A juvenile had ingested a small sliver of wood and a blade of dried grass.

TABLE II. Food of 57 *Coluber constrictor constrictor*

Food	Per cent of Occurrence		Per cent Volume	
Lizards (37)		64.9		61.4
Lygosoma laterale	35.1		34.2	
Eumeces fasiatus and *E. egregius*	14.0		11.3	
Cnemidophorus sexlineatus	8.8		8.8	
Sceloporus undulatus	3.5		3.5	
Undetermined species	3.5		3.5	
Snakes (16)		28.1		25.3
Opheodrys aestivus	7.0		6.6	
Diadophis punctatus	3.5		3.1	
Storeria dekayi	1.8		1.6	
Coluber constrictor	1.8		1.8	
Heterodon platyrhinos	1.8		1.8	
Masticophis flagellum	1.8		1.8	
Undetermined snakes	10.5		8.9	
Amphibians (5)		8.8		8.8
Rana	5.3		5.3	
Hyla cinerea	1.8		1.8	
Hyla versicolor	1.8		1.8	
Mammals (2)		3.5		3.5
Peromyscus	1.8		1.8	
Undetermined rodent	1.8		1.8	
Insects (Lepidoptera larvae) (1)		1.7		1.7

A comparison of the food of young (269-337 mm) snakes with that of large specimens indicates that the smaller individuals are generally restricted in their diet to small lizards, particularly *Lygosoma* and the young of *Eumeces.*

COACHWHIP SNAKE,

Masticophis flagellum flagellum SHAW

The coachwhip is one of the more abundant of the larger colubrids in the southeastern United States. Its abundance is attested by numerous road kills on southern highways and the appearance of many dead specimens following local fires. While this species is common within its range, little specific information is available on its food. Ditmars (1933) includes small rodents, birds and their eggs. Schmidt and Davis (1941) generalizing on the food of whipsnakes, include a wide variety of food, ranging from insects to birds and mammals. They include *Cnemidophorus* as an important food.

We have examined 51 specimens. Of these, 45 (88.2%) contained food (Table III). The snakes range in size from 329-1912 mm. Juveniles are easily recognized by the bright head colors and white scale borders. The young snakes utilize the same food as the larger adults, although smaller prey items are normally the lot of the juveniles.

TABLE III. Food of 45 *Masticophis flagellum flagellum*

Food	Per cent of Occurrence		Per cent Volume	
Lizards (31)		68.9		63.4
Cnemidophorus	51.1		42.2	
Lygosoma	8.9		8.9	
Eumeces	8.9		7.8	
Sceloporus	2.2		2.2	
Undetermined	2.2		2.0	
Mammals (8)		17.8		14.7
Sigmodon	13.3		10.2	
Blarina	2.2		2.2	
Mus	2.2		2.2	
Undetermined	4.4		.1	
Snakes (4)		8.9		8.9
Heterodon	2.2		2.2	
Diadophis	2.2		2.2	
Undetermined	4.4		4.4	
Insects (4)		8.9		8.3
Sphinx larva (*Xylophanes*)	6.6		6.6	
Undetermined lepid. larvae	2.2		1.6	
Bird (Savannah Sparrow)(1)		2.2		2.2
Turtle (*Kinosternon*) (1)		2.2		2.2

On January 15, 1951 a male in fine condition was taken. This snake, measuring 1556 mm and weighing 652 g, was coiled in a small mound of grass. The maximum and minimum temperatures for the day were 73° and 47° F, respectively. The stomach and intestinal tract was empty. In contrast, another male, collected on March 9, 1951, measured 1452 mm and weighed 341 g. It was thin, with lose skin, and had presumably recently emerged from hibernation. The stomach contained a savannah sparrow. Both *Eumeces laticeps* and *Eumeces egregius* were eaten by the coachwhips. A 1043-mm snake had eaten a newly hatched *Kinosternon subrubrum* with 25-mm carapace. The plastron was bright orange.

ROUGH GREEN SNAKE,

Opheodrys aestivus LINNAEUS

The rough green snake is essentially an insect feeder, securing much of its prey in bushes and vines which it frequently inhabits. Wright and Bishop (1915) include beetle larvae, a tree cricket and other orthopterous remains from three Georgia snakes. Van Hyning (1932) examined 17 Florida specimens, eight of which contained food. Insects were recovered from five stomachs, principally Lepidoptera, which constituted 53% of the bulk; spiders, principally lycosids, were taken from four stomachs, while one snake contained a frog. Uhler *et al.* (1939) report grasshoppers, cutworms, snails, phalangids and grasshoppers in two Virginia specimens. McCauley (1945) examined seven Maryland specimens and found grasshoppers, caterpillars and other undetermined insect remains, in addition to a single gastropod.

Forty-seven Benning specimens were examined (Table IV). Only a single one was without food, a remarkably high incidence of feeding. Specimens were taken from early June to October 29. They varied in size from 229-859 mm. All had a jet black peritoneum.

TABLE IV. Food of 47 *Opheodrys aestivus*

Food	Per cent of Occurrence		Per cent Volume	
Insects (45)		95.9		88.7
Orthoptera	72.4		55.1	
Locustidae	27.7		20.0	
Tettigoniidae	31.9		21.5	
Phasmidae	12.8		8.5	
Gryllidae	8.5		4.4	
Lepidoptera	42.8		32.5	
Coleoptera	2.1		trace	
Unidentified insects	4.3		2.2	
Arachnida (12)		25.5		9.5
Mollusca (4)		8.5		1.7
Crustacea (1)		2.1		.5

Most abundant of the Locustidae, *Schistocerca damnifica* occurred in eight specimens, while the tettigoniid *Scudderia furcata* was present in 5 specimens. Walking sticks, *Diapheromera femora,* were present in five snakes. Some of these insects were of large size, one measuring 126 mm in length. The Lepidoptera were represented by larvae of several families, including pierids, noctuids, and several species of sphingids, including *Xylophanes tersa.* Among the arachnids, egg masses of spiders were recovered from three individuals. Snails occurred in four stomachs, while traces of an isopod were recovered from one individual.

CORN SNAKE, *Elaphe guttata guttata* LINNAEUS

While the corn snake is a common species of the southeastern states, its specific food has not often been recorded. Ditmars (1936) records a quail that was disgorged by a specimen slightly over six feet in length. Wright and Bishop (1915) include rice rats, *Oryzomys,* in two Georgia individuals.

Thirty-six specimens were examined, of which 32 (88.8%) contained food. Those with food were collected from February 1 to November 2. The snakes ranged in total length from 256 to 1061 mm. A series of seven collected in August 1949 averaged 305 mm, while seven taken in October of the same year averaged 370 mm. The smaller snakes that contained food had usually eaten lizards and caterpillars, although the smallest individual examined (256 mm) contained a juvenile cotton rat that exceeded it in weight. The food analyses are recorded in Table V.

TABLE V. Food of 32 *Elaphe guttata*

Food	Per cent of Occurrence		Per cent Volume	
Mammals (19)		59.4		45.3
Peromyscus	18.8		15.3	
Sigmodon	15.6		13.7	
Cryptotis	3.1		3.1	
Undetermined	21.9		13.1	
Lizards (17)		53.1		45.6
Sceloporus	21.9		17.5	
Lygosoma	12.5		9.7	
Eumeces sp.	6.3		5.0	
Cnemidophorus	6.3		4.7	
Undetermined	9.4		8.7	
Insects (Lepidoptera larvae) (3)		9.4		5.9
Snake (1)		3.1		3.1

The abundance of lizards in the area is again reflected in the high incidence reported for this species. The single snake eaten appears to be *Carphophis,* although it was too well digested to permit positive determination. The insect larvae were all smooth, one being the common sphinx larva, *Xylophanes tersa,* of the region. The stomach of a 926-mm male contained a long conglomerated mass of rope fibers, dead grass stalks and leaves, with much impacted sand. The source of this material and why it was ingested is problematical.

GRAY RAT SNAKE, *Elaphe obsoleta spiloides* DUMÉRIL, BIBRON AND DUMÉRIL

This blotched constrictor is fairly common at Benning, 13 specimens being available for study. The gray rat snake commonly occurs in pairs. On several occasions, two specimens would be taken within a few days of one another, and at approximately the same site. Little has been recorded on the food of this race, although its feeding pattern does not appear dissimilar from the pilot black snake. Our specimens were taken from April 7 to October 7. The individuals range in length from 667-1823 mm. The date of capture, length of the specimen, and its food, are listed below.

Date	*Length, mm*	*Food*
April 7, 1952	1046	Robin
May 1, 1952	1823	*Peromyscus*
May 14, 1950	1608	Undetermined mammal

May 20, 1952	1191	Three nestling passerine birds
May 29, 1951	1393	Cotton rat (*Sigmodon*)
June 1, 1951	1316	Wood thrush
June 11, 1950	1209	Cotton rat
June 16, 1951	1202	*Cnemidophorus* and cotton rat
June 27, 1951	1813	Cottontail
July, 1950	1403	Cotton rat
July, 1950	1444	Undetermined small mammal
August 20, 1950	672	Cotton rat
October 7, 1951	667	Cotton rat

Mammals are the dominant food, occurring in three-fourths of the snakes examined. Even these large constrictors do not disdain the abundant lizards, as the presence of a *Cnemidophorus* in a stomach of one indicates.

Florida Pine Snake, *Pituophis melanoleucus mugitus* Barbour

Six specimens were collected, ranging in total length from 534 to 1622 mm. The occurrence of this snake at Fort Benning extends the known range considerably northward. Five of the six specimens contained food. The 534-mm individual had eaten a small *Carphophis*. Two contained cotton rat (*Sigmodon*) remains, another had eaten a *Cnemidophorus* and a small snake (smooth scales). A 1400-mm female collected on June 12, 1951, had eaten three snake eggs approximately the size and appearance of the two large eggs (57 x 18 mm) in its own oviduct.

Mole Snake, *Lampropeltis calligaster rhombomaculata* Holbrook

Three specimens of the mole snake were taken. One, a highway victim, taken July 1, 1951, had a length of 320 mm. It contained no food. Another, collected on September 20, 1950, was taken in the early morning. It was found in short grass on high ground. The hind gut contained remains of a cotton rat (*Sigmodon*). The third specimen was a road kill, with head and neck missing. Taken on November 2, 1950, it had usually large amounts of fat over the viscera. The hind gut contained the remains of a cotton rat.

Eastern King Snake, *Lampropeltis getulus getulus* Linnaeus

This constrictor, reputed to be a snake eater, lives up to its reputation in the few specific studies on its dietary. Wright and Bishop (1915) give some details of its fondness for other snakes and turtle eggs. They recovered a newly hatched *Heterodon* from one, and add that four specimens had eaten the eggs of *Chrysemys floridana,* while two had mud turtle eggs (*Kinosternon*) in their stomachs. Indeed, this species may wait on the turtle to lay its eggs, then uproot the clutch for a repast. Carr (1940) has observed Florida individuals feeding on cottonmouths and coral snakes. He watched a young king snake consume an eight-inch *Siren lactertina.* Schmidt and Davis (1941) include small mammals, lizards and amphibians.

Thirteen specimens containing food are available from Fort Benning. These were taken from March 8 to October 23. The dates, length and food are listed below.

Of the 13 specimens, 11 contained reptile remains, two had eaten mammals, while one contained a large sphingid larva. The food, other than the high incidence of lizards (46.2%), is in keeping with our knowledge of the usual diet of this species.

Date	*Length, mm*	*Food*
March 8, 1951	718	One 276-mm *Natrix sipedon fasciata* and an undetermined snake
April 22, 1952	1648	*Natrix erythrogaster*
May 1, 1950	1531	*Ophisaurus* 447 mm
May 1, 1950	781	*Cnemidophorus sexlineatus*
May 2, 1952	669	*Lygosoma laterale*
June 4, 1951	1126	Six snake eggs, *Coluber constrictor?*
June 6, 1951	1463	Four snake eggs, *Coluber constrictor?*
June 14, 1951	1186	*Eumeces fasciatus*
June 24, 1950	596	*Eumeces* sp. and fur
June 27, 1950	611	Snake, undetermined
July, 1950	1332	*Sceloporus*
Aug., 1949	1331	*Sigmodon*
Oct. 23, 1950	851	Sphinx larva, *Xylophanes tersa*

Scarlet Snake, *Cemophora coccinea* Blumenbach

Three specimens of this fossorial snake were taken. They range in length from 344 to 496 mm. The smallest contained the claws and scales of *Lygosoma laterale,* fragmentary remains of a small caterpillar and undetermined insect remains. Presumably the insects were of secondary origin. The largest snake, collected April 22, 1952, contained sand and detritus in the hind gut, possibly from an earthworm. Another, taken on April 25, 1952, was plowed up at an estimated depth of 8 inches. It contained no food.

CROWNED SNAKE, *Tantilla coronata coronata* BAIRD AND GIRARD

This small snake appears to be a specific feeder, restricting its diet to centipedes when these are available. Force (1935) examined the stomachs of 63 specimens of *Tantilla gracilis,* and found the principal food to consist of centipedes and earth-dwelling insect larvae, as cutworms, wireworms, and the larvae of craneflies. This boigid is included with the colubrids because of its abundance in the study area.

Twenty-six specimens were examined, of which 20 contained food. The snakes ranged from 106 to 287 mm in length. Centipedes occurred in 17 specimens, while beetle larvae were present in two, and blattids and millipedes each in a single snake. One large crowned snake (227 mm) was taken from a well rotted moist pine log on March 2, 1951. It had eaten a 56-mm centipede.

Crowned snakes were kept in captivity for several months. All fed exclusively on centipedes, although a variety of insect larvae, termites, ants, isopods and millipedes were offered. The snakes burrowed through the friable soil of their quarters, seldom appearing on the surface either during the day or night.

SUMMARY

The food of 367 colubrid snakes of 23 species from the Fort Benning Military Reservation, Georgia is recorded. Lizards are particularly abundant on the study area and are an important food of the larger snakes. Of 134 specimens of *Coluber constrictor, Masticophis flagellum* and *Elaphe guttata,* lizards had been eaten by 85 (63.4%). Snakes, mammals, amphibians and insects are the other primary foods. *Tantilla* appears to be a specific feeder, taking centipedes when these are available.

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STUDIES ON THE ECOLOGY OF DROSOPHILA IN THE YOSEMITE REGION OF CALIFORNIA

I. THE OCCURRENCE OF SPECIES OF DROSOPHILA IN DIFFERENT LIFE ZONES AND AT DIFFERENT SEASONS

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INTRODUCTION

The genus *Drosophila* contains more than 600 described species. As far as known, most of them subsist on yeasts and bacteria which occur in plant materials rich in carbohydrates. Drosophila is ecologically a rather highly specialized but closely knit group which offers valuable opportunities for studies on organism-environment relationships. In many habitats, especially in the tropics, several dozen Drosophila species may occur side by side. Only 14 species have been recorded in the Yosemite Park region of the Sierra

Nevada Mountains of California (Table I). This makes a manageably small group which can be conveniently studied.

Observations on species of Drosophila in the Yosemite Park region have been made during the summers of 1945, 1946, 1947, 1950, 1951, and 1954 (see Dobzhansky 1948, 1951, 1952, Dobzhansky and Wright 1947, Carson 1951, da Cunha, Dobzhansky and Sokoloff 1951). This region contains a considerable diversity of environments, varying in a fairly regular fashion with altitudes from near sea level to a crest of up to 13,000 feet. Collections of Drosophila have been made at altitudes ranging from 850 feet (Upper Sonoran life zone) to about 11,000 feet (boundary of Hudsonian and Arctic-Alpine life zones). The observational and experimental data bearing on the ecology of Drosophila in the Yosemite region are reported in the following series of four articles, of which the present one is intended to give a brief account of the composition of the Drosophila fauna in the different habitats and of its dependence on the climatic and biotic variables.

Collecting Techniques

Almost all collections of Drosophila dealt with in this article have been made by exposing bait consisting of banana fermented with yeast and capturing the flies which are attracted to the bait. Much smaller collections have been made on slime fluxes on oak trees (Carson 1951), and on fungi. In the period of 1945-1951 the banana bait was exposed in 3½ x 2½ inch "drinking cups" of paper or of plastic placed on wire stands. Ripe bananas were mashed and inoculated mostly with the ordinary Fleischmann's yeast. In 1954 cans of 6 x 8 inches were used; about one pound of bananas were placed in each can, autoclaved, inoculated with various yeasts (see the following paper by Dobzhansky *et al.*), and exposed standing on the ground to attract the flies. Almost all exposures of the bait were made either during the late afternoon hours or during the morning hours when the flies are active (Dobzhansky and Epling 1944). At other times the bait was kept in closed containers which prevented it from drying out. The flies were collected at intervals, either with the aid of a collecting net (for larger cans) or of a glass funnel (for smaller cups). Equal numbers of collections were made in all traps. The captured flies were etherized and classified by examining them under a binocular microscope usually within a few hours, or always within a day from the time of capture. Certain species, particularly *Drosophila pseudoobscura* and *Drosophila persimilis* cannot be distinguished by such inspection, nor can females of these species be reliably distinguished from females of *Drosophila azteca.* The females of all three species were, accordingly, scored together as "*obscura* group females." Males of *Drosophila pseudoobscura* and *Drosophila persimilis* were scored together as "*pseudoobscura* and *persimilis* males," while *Drosophila azteca* males were recorded separately. In 1954 most of the *Drosophila pseudoobscura* and *Drosophila persimilis* males were classified later by examination of their genitalia in specimens cleared for 12-24 hours in a 5% potassium hydroxide solution and placed in a drop of glycerine. Apart from the difference in the proportion of the penis described by Rizki (1951), these species also differ in the shape of the hypandrium. This difference has been observed first by Dr. R. Lewontin and D. M. Cooper and it permits a relatively clear-cut separation of the otherwise morphologically almost identical species. When flattened under a cover slip the hypandrium of *D. persimilis* is straight sided and more rectangular in appearance than that of *D. pseudoobscura,* the latter being tapered distally from the end to which the penis is attached. Coupled with this character is the small acute projection of the hypandrium of *D. persimilis* shown in Figure 2 in Rizki (1951). Under similar treatment the corresponding part of the hypandrium of *D. pseudoobscura* does not form an acute projection.

The Collecting Localities

General descriptions of the geographic, climatic, and biotic characteristics of the region in which our collections have been made can be found in Grinnell and Storer (1924) and in Clausen, Keck and Hiesey (1940). The following brief descriptions of the collecting localities will, then be sufficient.

Lost Claim Camp Ground in Stanislaus National Forest, 3000 feet above sea level. The lower part of the Transition life zone. Characteristic trees are *Pinus ponderosa, Libocedrus decurrens,* and *Quercus kelloggii.* Along the banks of the stream are some *Alnus rhombifolia* and *Acer macrophyllum.*

Mather, 4800′, in Stanislaus National Forest near the experimental gardens of the Carnegie Institution of Washington. Transition life zone. The trees of this area are the same as those at Lost Claim, except that there is no *Alnus* or *Acer.*

Aspen Ranger Station in Yosemite National Park, 6000′. Upper limit of Transition life zone. *Pinus ponderosa* var. *jeffreyi, Pinus lambertiana, Abies concolor,* and a few *Quercus kelloggii* present.

Aspen Stream is about two miles east of Aspen

Ranger Station, 6400′. Near the ecotone between the Transition and the Canadian zones. *Abies concolor* is the dominant tree of the hillsides with specimens of *Pinus ponderosa* var. *jeffreyi* and *Pinus lambertiana* present. In the valley of the stream, aspen, *Populus tremuloides,* is the dominant species.

Smoky Jack Camp Ground in Yosemite National Park, 7500′. Near the ecotone between the Transition and the Canadian zones. The dominant tree species here is *Abies magnifica,* with *Abies concolor* and *Pinus contorta* in relatively small numbers.

White Wolf Camp Ground, 8000′. Canadian life zone, where the dominant tree is *Pinus contorta.* A few saplings *Abies magnifica* in the collecting area, but all under eight feet high. Some willow, *Salix* sp., occurs along the banks of a stream.

Yosemite Creek Camp Ground, Yosemite National Park, 7200′. Although the altitude of this locality is relatively low, the effect of cold air drainage produces a vegetation typical of the Canadian life zone with *Pinus contorta* being the dominant tree.

Porcupine Flat, Yosemite National Park, 8200′. The forest in the collecting area is pure *Pinus contorta.* Canadian life zone.

Timberline, Inyo National Forest, 10,000′. Near the experimental gardens of the Carnegie Institution of Washington, about 350-800 feet below the true timberline. *Pinus contorta* and *Pinus albicaulis* in the Hudsonian life zone.

ALTITUDINAL DISTRIBUTION

Fourteen species of Drosophila and one species of *Aulacigaster* have been recorded in the Yosemite region. The total numbers of individuals of these species in our collections are shown in Table I. These numbers do not accurately reflect the population densities in the localities sampled. In the first place, the number of collections made at Mather is greater than that at Aspen, and that is much greater than at other localities which were sampled only once or twice each. Moreover, the bulk of the data are derived from collections made in 1954, and the relative frequencies of the species are known to vary from year to year. Finally, as shown by Dobzhansky and Pavan (1950), the relative frequencies of the different species vary with the nature of the bait used. Nevertheless, Table I does show some salient facts concerning the altitudinal distribution of the flies.

Thus, *Drosophila azteca* Sturtevant and Dobzhansky is commonest in the lower reaches of the Transition zone, and becomes rare or absent as the Canadian zone is appoached. It is also rare in the Upper Sonoran zone, as shown by the collections at Jacksonville at the elevation of 850 feet. Unfortunately no exact records of the collections made at Jacksonville in 1946-1951 have been preserved, and they are accordingly not included in Table I. In 1947 and 1951, *Drosophila azteca* was found to be exceedingly abundant in late summer also in Pate Valley, 4200′, which has a lower Transition zone vegetation.

Drosophila occidentalis Spencer and *Drosophila pinicola* Sturtevant are both absolutely and relatively the most abundant species in the upper part of the Transition and in the Canadian zones. *Drosophila occidentalis* still occurs, however, in the Hudsonian zone: apart from the localities shown in Table I, this species has been found at Lyell Base Camp (10,800′), in upper Matterhorn Canyon (9500′), and in Virginia Canyon (9000′). *Drosophila californica* Sturtevant is relatively commonest in the upper portion of the Transition

Table I. Numbers of individuals of different species of Drosophila collected at different stations

Species	Lost Claim	Mather	Aspen Ranger Station	Aspen Stream	Smoky Jack	White Wolf	Yosemite Creek	Porcupine	Timberline
obscura group ♀♀	126	14,125	1,487	613	195	25	13	40	40
pseudoobscura and *persimilis* ♂♂	58	8,862	897	284	145	31	13	32	45
azteca ♂♂	108	10,087	667	21	7	1	...	...	...
miranda	...	473	556	364	185	29	9	12	6
occidentalis	23	2,490	1,948	19,296	11,127	137	514	266	42
pinicola	24	2,561	5,626	4,546	2,752	207	85	419	20
melanogaster	...	2,926	4	...	159	...	...	...	...
busckii	...	12	...	...	1	2	...	...	...
immigrans	10	27	...	...	...	...	...	...	...
hydei	...	5	...	...	...	...	...	...	...
californica	1	119	234	17	5	4	...	2	...
subfunebris	...	61	5	...	...	...	...	...	...
victoria	...	72	...	...	...	...	...	...	...
montana	...	1	...	7	1	5	76	5	...
Aulacigaster sp.	8	844	114	26	...	...	...	...	...

zone (Aspen), although it extends also into the Canadian and rarely into the Upper Sonoran zones. *Drosophila victoria* Sturtevant has been recorded only from Mather and from Jacksonville (the latter record not included in Table I). *Aulacigaster sp.* is confined to the Transition and Upper Sonoran zones. According to Carson (unpublished) this fly is breeding in sap exudations of many trees, including *Quercus kelloggii, Q. chrysolepis, Abies concolor, Alnus rhombifolia, Populus tremuloides,* and *Salix sp.* The altitudinal range of *Drosophila montana* Patterson is given by Patterson (1943) as being 4500-10,000′, and this agrees with our data. This species is found only near streams along which grow aspens or willow trees. The relatively large number of this species recorded for Yosemite Creek (Table I) is due to a collection made by Carson near fallen aspen trees at that locality (see Carson, Knapp, and Phaff 1956, the third paper of the present series).

The four species, *Drosophila melanogaster* Meigen, *Drosophila busckii* Coquillett, *Drosophila immigrans* Sturtevant, and *Drosophila hydei* Sturtevant are introduced into the Yosemite region by man. They are found in this region irregularly, and only near public camp grounds or other places of human habitation. Thus *Drosophila melanogaster* was found at Mather only rarely towards the end of the summer in 1947, 1950, and 1951, and not at all in 1945 or 1946. In 1954 this species was absent or rare in June and July, but suddenly became extremely abundant in late August and in September. On the contrary, *Drosophila busckii* was fairly common in late summer in 1950 and 1951, but not in 1954. The altitudinal distribution of *Drosophila pseudoobscura Frolowa* and *Drosophila persimilis* Dobzhansky and Epling will be discussed below.

Seasonal Variations

Collecting Drosophila at different seasons in the same locality discloses that the abundance of the different species changes greatly with time. Table II summarizes the relevant data for the summer of 1954, during which the collections were most abundant and complete records were kept. The species clearly associated with man (*D. melanogaster, D. immigrans, D. busckii,* and *D. hydei*) are not included in the table. These species are collected chiefly in late summer, and are rare or absent in June. In the early October collections at Mather *D. melanogaster* was decidedly the dominant species (this collection is not included in Table II).

D. occidentalis has shown the most pronounced change in abundance with season in 1954 and also in other years. At Mather this species was abundant in June but relatively rare in August and September. At Aspen the peak of abundance

Table II. Changes in the relative frequencies of different species of Drosophila with time. The figures show the percentage incidence of each species among the total number of Drosophila collected during a given period

Locality and Date	*obscura* group ♀♀	*pseudoobscura* and *persimilis* ♂♂	*azteca* ♂♂	*miranda*	*occidentalis*	*pinicola*	*californica*	*subfunebris*	*victoria*	*Aulacigaster* sp.	*montana*	Flies classified
Mather												
6. 1-7.54......	38.59	17.57	11.01	0.73	12.81	17.45	0.02	....	....	1.80	0.02	5457
6.15-20.54.....	41.02	18.93	13.16	0.41	11.17	14.46	0.04	0.12	....	0.69	....	2462
7. 2-8.54.....	49.62	18.69	19.11	0.70	6.24	3.97	....	0.16	0.02	1.50	....	5725
7.16-20.54.....	45.75	15.24	25.93	0.92	7.39	2.69	0.10	0.10	0.29	1.57	....	4789
8. 6-10.54.....	46.27	12.45	30.17	3.29	2.61	2.61	0.35	0.07	0.13	2.03	....	5373
8.20-27.54.....	34.22	16.80	32.38	1.69	5.49	8.28	0.22	0.15	0.10	0.69	....	4083
9. 3-10.54.....	31.86	22.64	33.23	0.99	4.35	3.82	0.65	0.14	0.30	2.02	....	6573
Aspen R. S.												
6.14-16.54.....	8.63	5.70	0.61	2.27	9.74	70.95	0.76	....	....	1.34	....	3962
7.20-22.54.....	17.82	4.96	8.28	10.79	16.41	39.70	1.35	0.04	....	0.68	....	2559
8.10-12.54.....	28.22	12.30	7.36	7.48	10.40	29.23	4.38	....	....	0.63	....	1577
8.23-24.54.....	23.00	9.05	5.75	4.24	8.86	47.31	1.51	....	....	0.28	....	1061
Aspen Stream												
6.17-19.54.....	6.20	3.32	0.05	1.16	34.01	54.60	0.13	....	....	0.53	....	3949
7. 5-7.54.....	0.78	0.34	0.10	1.08	88.42	9.24	0.02	....	....	0.03	....	17474
8.28.54........	6.19	2.51	0.03	3.47	66.73	20.69	0.21	....	....	....	0.19	3751
Smoky Jack												
6.29.54........	4.63	3.83	0.27	1.49	56.37	33.22	0.19	....	....	....	....	2613
8.31.54........	0.63	0.38	....	1.24	81.79	15.96	....	....	....	....	0.01	11804

TABLE III. Proportions of *Drosophila azteca* in collections of *D. pseudoobscura, D. persimilis* and *D. azteca* males

Locality	Date of collection	Males classified	Percent *azteca*
Jacksonville	6.18.46	36	0.0
	7.21.46	31	0.0
	5.15.47	70	9
	6.21.47	52	2
	7.31-8.1.47	101	1
	9.8.47	92	24
	2.17.48	78	44
	3. 7.48	39	46
	5.15.48	15	40
Lost Claim	6.24-26.46	167	16
	8.11.46	171	71
	5.15.47	135	76
	6.30.47	343	47
	8.30.47	381	60
	9. 9.47	315	71
	7.10.54	166	65
Mather	6. 8-15.45	547	36
	8.10.45	167	39
	8.22-9.5.45	1134	50
	6. 4-15.46	718	18
	6.26-30.46	201	30
	8. 9-10.46	227	45
	6.22-26.47	188	12
	7.26.47	584	34
	9. 1- 4.47	1139	77
	9.12.47	393	68
	6.29.50	314	32
	7.25-28.50	285	35
	8.18-27.50	890	42
	6.25.51	87	33
	7. 6-19.51	481	25
	8.10-26.51	407	43
Mather	6. 1- 7.54	1560	39
	6.15-20.54	790	41
	7. 2- 8.54	2164	51
	7.16-20.54	1972	63
	8. 6-10.54	2290	71
	8.20-27.54	2008	66
	9. 3-10.54	3672	60
Aspen R. S.	6.30.46	96	46
	7. 6- 9.46	65	15
	6.19-26.47	63	11
	8.31.47	25	80
	9. 4-11.47	153	72
	7.13-17.51	101	18
	7.22.51	128	56
	8.13.51	263	58
	8.22-24.51	16	69
	6.14-16.54	250	10
	7.20-22.54	339	63
	8.10-12.54	310	37
	8.23-24.54	157	39
Aspen Str.	7.8.46	21	0
	6.17-19.54	133	2
	7. 5- 7.54	77	23
	8.28.54	95	1
Smoky Jack	6.29.54	107	7
	8.31.54	45	0
White Wolf	6.28.54	32	3
Yosemite Cr.	7.8.54	13	0
Porcupine Flat	7.13-14.46	21	0
	7. 8.51	35	0
	6.25.54	32	0

was reached later in July, and at Smoky Jack, where this species occurs in great numbers, in August. This species is most commonly found in more humid areas; thus, at Aspen Stream it came in much greater numbers to the traps placed in a ravine with a small stream lined with aspen trees than to those on the adjacent hillside with *Abies* as the dominant tree. This species has also been collected near mushrooms belonging to the genera *Clavaria* and *Pleurotus* at Aspen Stream and at Smoky Jack. According to Patterson (1943) fungus-breeding Drosophila have population peaks during the wetter seasons when more fungi are available. It may be that during the dry summer climate of the Yosemite region a proximity to streams results in a greater abundance of the preferred food and of breeding places of this species.

D. pinicola is most abundant early in the season. The species has been observed visiting slime fluxes of oaks and *Abies concolor* (Carson 1951; Carson, Knapp and Phaff 1955). This species was reared from *Clavaria* fungus. If it breeds on fungus there is no reason why it should not be abundant at Aspen Ranger Station, especially if it can maintain itself by feeding on bacteria from *Abies* fluxes.

The abundance of *D. azteca* increases toward the hottest part of the summer (late July and early August). This is clear from the data in Table II, and even more so from those in Table III, which summarizes the information concerning the abundance of *D. azteca* relative to that of the *obscura*-like sibling species (*D. pseudoobscura* and *D. persimilis*) for various years beginning with 1946. However, several facts may be noted in this connection. First the abundance of *D. azteca* varies from year to year. It was not recorded at all in 1946 at Jacksonville, but was quite common there early in the season in 1948. At

Mather it was less common in 1945, 1946, 1950 and 1951 than in 1947 and 1954. Secondly, its altitudinal distribution is not what could be expected of a species which builds its greatest population at Mather during the hottest part of the summer. Indeed, it was rare at Jacksonville except during the spring of 1948, evidently being depressed by the high summer temperatures of the Lower Sonoran zone. But it is also rare or absent in the Canadian and Hudsonian zones. Yet in Mexico and in Guatemala, *D. azteca* occurs alone in the tropical lowlands, while at higher elevations *D. pseudoobscura,* is found together with *D. azteca* or alone (Dobzhansky and Epling 1944).

The relative frequencies of the sibling species *D. pseudoobscura* and *D. persimilis* are compared in Table IV. Females of these species were discriminated by examination of the chromosomes in the salivary gland cells of the larvae in their progeny (see Dobzhansky and Epling 1944), while the discrimination of the males was made by examination of their genitalia (see above). Both species are abundant in the Transition zone. At higher elevations, however, *D. persimilis* is much more common than *D. pseudoobscura,* while at lower elevations the reverse is the case. Seasonal fluctuations at Jacksonville and Lost Claim show an expected decrease in the relative frequency of *D. persimilis* during the hotter part of the summer.

TABLE IV. Relative abundance of *Drosophila pseudoobscura* and *D. persimilis*

Locality	Date of collection	Total females classified	Percent pseudo-obscura
Jacksonville	6.18.46	101	99
	7.20-21.46	67	100
	4.13.47	31	81
	5.15.47	131	95
	6.20-21.47	100	100
	7.31.47	105	96
	9. 7.47	68	82
Lost Claim	6.24.46	76	88
	8.11.46	68	91
	5.15.47	104	68
	6.20.47	87	84
	8. 6.47	99	98
	9. 9.47	40	25
Mather	7. 8-15.45	155	63
	8.22-9.5.45	543	60
	5.15.47	59	59
	6.22-26.47	100	61
	7. 5.47	66	79
	7.26.47	116	86
	9. 1-12.47	110	55
	6.29.50	68	70
	7.25-28.50	57	70
	8.18-27.50	141	49
	6.26-30.51	56	89
	7. 1-15.51	132	89
	7.16-30.51	57	95
	8. 7-16.51	38	97
	5.30-6.6.54	460	58
	6.15-17.54	174	39
	7. 2- 4.54	140	70
	7.17-19.54	198	74
	8. 6-10.54	251	69
	8.20-27.54	247	68
	9. 3-10.54	757	28
	10.?.54	103	22
Aspen R. S.	7. 6- 9.46	117	54
Aspen Str.	6.19-25.47	109	58
	7.29.47	104	72
	8.31-9.11.47	94	40
	6.15-19.54	125	40
	8.23-28.54	99	26
Porcupine Flat	7.13-14.46	44	7
	7.11-17.47	77	21
Timberline	7.24.46	17	12

Locality	Date of collection	Total males classified	Percent pseudo-obscura
Lost Claim	7.10.54	55	78
Mather	6. 4-15.46	2065	66
	8. 9-10.46	79	29
	6. 1- 7.54	845	57
	6.15-20.54	448	60
	7. 2- 8.54	972	53
	7.16-20.54	675	57
	8. 6-10.54	639	64
	8.20-27.54	625	54
	9. 3-10.54	1187	62
Aspen R. S.	6.14-16.54	197	47
	7.20-22.54	123	34
	8.10-12.54	180	54
	8.23-24.54	84	35
Aspen Str.	6.17-19.54	114	40
	7. 5- 7.54	58	21
	8.28.54	77	47
Smoky Jack	6.29.54	87	21
	8.31.54	29	17
White Wolf	6.28.54	31	10
Yosemite Cr.	7.8.54	13	0
Porcupine Flat	6.25.54	32	19
Timberline	6.24.54	45	2

At Mather, on the other hand, variations in the relative frequencies of these species are erratic not only from year to year but within seasons. The 1954 collections show a rather regular change in the frequencies; *D. pseudoobscura* females reach a peak in mid-July, while *D. persimilis* females become very common in the September and October collections. This change in frequency was not, however, reflected among the males.

VARIATIONS IN THE SEX RATIO

Most collections of *D. pinicola* made in 1954 contained considerably more females than males (Table V). Unfortunately no sex ratio records were made in previous years, and it is not certain that the preponderance of females is a constant feature in this species. Indeed, the collections made at Aspen Stream seem to show a much less pronounced scarcity of males than those at Aspen Ranger Station only some 3 miles away (Table V). The origin of this abnormality of the sex ratio is unknown. Nothing quite comparable to it was observed in 1954 in any other Drosophila species. The data in Table II suggest, however, that among the species of the *obscura* group collected at Mather the females were somewhat more frequent in late August and in September. It is not very likely that these apparent changes in the sex ratios reflect actual frequencies of the two sexes in its natural populations. A more probable, though unproven, explanation is that under some conditions the attractivity of the bait may not be alike for the females and males of the same species, and that the reaction of the sexes to bait may undergo changes with the season.

TABLE V. Percentages of females in the collections of *Drosophila pinicola*

Locality	Date of collection	Percent females	Flies classified
Mather	7. 2- 8.54	90	227
	7.16-20.54	78	129
	8. 6-10.54	88	140
	8.20-27.54	91	338
	9. 3-10.54	78	251
Aspen Ranger Station	7.20-22.54	80	1016
	8.10-12.54	83	461
	8.23-24.54	74	502
Aspen Stream	7. 7.54	67	465
	8.28.54	51	776

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CONCLUSIONS AND SUMMARY

The species of Drosophila which inhabit the Sierra Nevada Mountains in the Yosemite region of California are differentiated with respect to their adaptedness to environmental variations in space and in time. Although some of the species occur at all elevations at which collections have been made (from 850 to 11,000 feet), every species is relatively more abundant in some altitudinal zones than in others. Some species appear to be more narrowly specialized than others, and do not occur at all at some altitudes although they are abundant at other altitudes. Within a locality, the relative abundance of different species varies from season to season and from year to year. The causes of such temporal variations are obscure. A species (such as *Drosophila azteca*) which in some localities is most abundant during the hottest season of the year is not necessarily abundant at lower elevations where the seasonal temperatures are higher than they are at higher elevations.

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STUDIES ON THE ECOLOGY OF DROSOPHILA IN THE YOSEMITE REGION OF CALIFORNIA

II. YEASTS FOUND IN THE ALIMENTARY CANAL OF DROSOPHILA

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The study of yeasts associated with wild species of Drosophila has received increasing atttention in recent years. This interest was stimulated on the one hand by the discovery of the importance of yeasts as a nutrient for Drosophila and the possible role of nutrition in population changes, the striking differential attractivity of various species of yeast to different species of Drosophila, and on the other hand by the greatly improved yeast systematics and the consequent renewal of interest in yeast ecology. Shehata, Mrak and Phaff (1955) reviewed the literature dealing with yeasts isolated from Drosophila. Most of the earlier work is limited in scope and in most cases identification of the yeast to species was incomplete or omitted. This is, for example, the case in a recent study by Dudgeon (1954) who identified only to genus 130 yeasts, obtained from 21 species of Drosophila collected in 12 different states of the United States. Her yeasts belonged mostly to *Debaryomyces, Hansenula, Pichia, Saccharomyces, Candida, Kloeckera* and *Torulopsis.* No seasonal or geographic variation in these genera could be found. A survey of yeasts identified only to genus is of limited value, since it has become more and more evident that ecological niches which can support the growth of yeast, usually contain highly specific types of yeast. The work of Shehata *et al.* (1955) concentrated primarily on the yeasts associated with *obscura* group flies in southern California, although some exploratory work was also done with *obscura* flies at Jacksonville and at Mather in the Sierra Nevada of central California. Three new species of yeast were described, which all had the characteristic kidney- or crescent-shaped ascospores. *Saccharomyces drosophilarum* was found in both areas, and *S. phaselosporus* and *S. dobzhanskii* only at Pinon Flats, in southern California.

The present investigation was undertaken to explore more thoroughly the yeasts occurring in the crops of adult specimens of the common species of Drosophila and Aulacigaster found in the Mather region. In addition a somewhat more limited study was made of various areas at higher altitudes. Occasional samples were also taken from relatively rare species.

Experimental Methods

Bait for Drosophila. Most of the flies were captured after they were attracted to cups containing banana mash, fermented by bakers yeast, in which the yeast was subsequently killed by treatment with ethylene oxide (Phaff 1955). This bait, which is sterile and non-toxic, avoids the danger that flies consume live bakers yeast before capture. During the early part of the work live yeast bait was used in a few collections and a number of typical bakers yeast cultures were isolated from the flies. These isolations are disregarded in this paper, since flies caught by means of the sterile bait never yielded a single culture of typical bakers yeast.

Dissection of the flies. With respect to *D. pseudoobscura, D. persimilis* and *D. azteca,* only males were studied, since the females of these species cannot be distinguished by gross morphology. Males of *D. azteca* can be recognized readily by their single sex comb, but males of the first two species, which both have double sex combs, were identified in a number of instances, after dissecting out the crop, through the kindness of Dr. M. T. M. Rizki, for which we express our thanks. All flies were dissected within about one hour after being trapped to avoid digestion of their yeasts (Shehata and Mrak 1951). The flies were anaesthetized with ether and placed in a droplet of sterile water on a sterile slide. The crop was removed with the aid of two sterilized dissecting needles and the isolated crop was rinsed twice in sterile water. It was then placed on an agar plate in a drop of sterile water.

The crop was then crushed with a loop and the resulting suspension evenly streaked over the plate.

Isolation of the yeasts. Wort agar of 5° Balling was used for streaking. The yeasts were purified by the customary plating technique. Mold contamination was rarely encountered. Bacteria frequently accompanied the yeasts; some plates contained only bacteria and still others produced no growth at all. Bacteria, however, were not isolated in the present study. The yeast colonies which appeared on a plate were inspected carefully with a wide-field microscope and those which showed differences in colony morphology were isolated. If later two or more isolations from the same plate (and therefore from the same fly) were found to be identical species, they are reported as single isolations. Some, although not many, species of yeast are nearly indistinguishable by colony morphology. Since often as many as 500 colonies of yeasts appeared on a single plate, it is obviously not possible to select more critically than by visual inspection. The third plating usually produced a pure culture and this plate was kept and periodically inspected for ascospore production, since it was found that a high percentage of the sporogenous yeasts formed spores on wort agar and did not require a special sporulation medium.

Identification of the yeasts. The yeasts were identified by the system of Lodder and van Rij (1952) except that the number of carbon compounds used to determine their assimilation characteristics was greatly expanded to include most of the compounds used by Wickerham (1951) in his study of the genus *Hansenula.* Species belonging to this genus were identified by the system of Wickerham (1951). Organisms which could not be identified with previously described species are indicated as new species and will be described in detail in a separate publication in the journal Antonie van Leeuwenhoek (1956 No. 2).

TABLE I. Yeasts isolated from Drosophila in the Yosemite Region of California.

Species of yeast	No. of isolates	Areas in which isolated
SPORULATING YEASTS		
†*Saccharomyces montanus* Naganishi nov. comb.	36	M; PF
†*S. veronae* Lodder et van Rij 1952	30	M; AV; T
†*S. cerevisiae* Hansen var. *tetrasporus* (Beijerinck) nov. comb.	22	M
†*S. drosophilarum* Shehata, Mrak et Phaff 1955	13	M
†*S. drosophilarum* Shehata, *et al.* var. *acellobiosa* nov. var.	2	M
†*S. florentinus* (Castelli) Lodder et van Rij 1938	2	M; PF
†*S. pastori* (Guilliermond) Lodder et van Rij 1919	2	M
†*S. wickerhamii* nov. spec.	2	YC; AV
S. pini (Holst) Shifrine et Phaff 1936	1	M
†*S. dobzhanskii* Shehata, Mrak et Phaff 1955	1	PF
†*S. uvarum* Beijerinck 1898	1	PF
†*S. kluyveri* nov. spec.	1	M
†*Hansenula angusta* Wickerham 1951	19	M; AV; PF
†*Pichia fermentans* Lodder 1932	2	M
Pichia xylosa nov. spec.	1	M
P. membranaefaciens Hansen 1888	1	M
†*Hanseniaspora valbyensis* Kloecker 1912	6	M
†*H. uvarum* (Niehaus) Shehata *et al.* 1932	6	M
†*H. osmophila* (Niehaus) nov. comb. 1932	5	M
NON-SPORULATING YEASTS		
†*Kloeckera apiculata* (Reess *emend.* Kloecker) Janke 1870	15	M; PF; T
†*K. magna* (De'Rossi) Janke 1920	13	M
†*Torulopsis stellata* (Kroemer et Krumbholz) Lodder 1931	10	M; PF; T
†*T. glabrata* (Anderson) Lodder et de Vries 1917	1	AV
T. pinus Lodder et van Rij 1952	1	AV
T. inconspicua Lodder et van Rij 1952	1	AV
†*T. colliculosa* (Hartmann) Saccardo 1903	1	M
Cryptococcus diffluens (Zach) Lodder et van Rij 1934	5	M; YC; T
Cr. laurentii (Kufferath) Skinner 1920	2	M; PF
Rhodotorula aurea (Saito) Lodder 1934	1	PF
Rh. minuta (Saito) Harrison 1922	1	AV
Rh. glutinis (Fres.) Harrison 1852	1	M
Rh. mucilaginosa (Jörg.) Harrison 1909	1	PF
†*Candida krusei* (Cast.) Berkhout 1910	10	M; AV
†*C. catenulata* Diddens et Lodder 1942	6	AV
†*C. parapsilosis* (Ashf.) Lang. et Talice var. *intermedia* van Rij et Verona 1949	6	SJ
†*C. parapsilosis* (Ashf.) Lang. et Talice 1928	2	M; AV
C. mesenterica (Geiger) Diddens et Lodder 1910	4	M; PF; T
C. mycoderma (Reess) Lodder et van Rij 1870	2	M; PF
†*C. guilliermondii* (Cast.) Lang. et Guerra 1912	1	M
Trichosporon aculeatum nov. spec.	2	AV; T
†*Tr. fermentans* Diddens et Lodder 1942	1	M
Oospora lactis (Fres.) Saccardo	1	M
Total number of isolates	242	....

*Areas studied are indicated as follows: M = Mather area; AV = Aspen Valley; SJ = Smoky Jack; YC = Yosemite Creek; PF = Porcupine Flat; T = Tioga Pass area.
†Indicates moderately or strongly fermentative yeasts.

RESULTS

Most of the flies were collected at Mather and some also at Aspen Valley, Smoky Jack, Yosemite Creek, Porcupine Flat and at Tioga Pass near Timberline. For characterization of these localities see the preceeding paper of Cooper and Dobzhansky.

The names, number of isolates and areas in which the yeasts were found are listed in Table I. The yeasts are arranged by genera, and in the order of their frequency of occurrence. It can be seen that the genus *Saccharomyces* is by far the most widely represented, both in number of species and in total number of isolates. The apiculate yeasts (yeasts with lemon-shaped cells), represented by the genera *Hanseniaspora* and *Kloeckera,* were also common. It might be pointed out that *Kloeckera apiculata* is believed to be the imperfect form of *Hanseniaspora valbyensis* or *H. uvarum. Kloeckera magna* is probably the imperfect form of *H. osmophila.* This means that these speices are morphologically and physiologically indistinguishable, unless sexual spores are produced. This is of interest, since some representatives of such pairs of species gave different attractivity to some species of *Drosophila* (see the concluding paper of this series). Other common yeasts are *Hansenula angusta, Torulopsis stellata* and *Candida krusei.* All species of the common genera are good fermenters, many species, in fact can ferment a variety of sugars. A great majority of the other yeasts cannot ferment at all, or they only ferment glucose weakly. This generalization has two exceptions in the genus *Saccharomyces. S. pini* and *S. pastori* (especially the first) are weak fermenters. It is, however, doubtful if these two species properly belong in the genus *Saccharomyces,* since both produce hat-shaped spores a morphological feature not found in any other species of *Saccharomyces.* This consideration will be taken up in more detail in our taxonomic paper.

Since the emphasis of this paper is on the relation of the yeasts to the various species of Drosophila, we have listed in Tables II, III, IV and V the yeasts isolated from Drosophila at Mather, Aspen Valley, Porcupine Flat and Tioga Pass, respectively. Included in the tables are the total numbers of dissected flies of each species and the number yielding one or more yeasts. Since not all *obscura* group flies (*D. pseudoobscura* and *D. persimilis*) were identified to species, a separate column is included in Table II listing these sibling species combined. It can be seen that the most thorough investigation was made in the Mather area. Of the 216 flies dissected 137 contained yeasts and 79 had no yeasts in their crops. Of the last group only 15 flies yielded no growth and the rest had only bacteria, often in large numbers. The most significant observation to be derived from Table II is that all common species of flies contained nearly all of the major species of yeast. This includes *D. pinicola,* which is found in fair numbers at Mather, but is much more common at the higher altitudes. It will be noted that 31 out of 55 *D. pinicola* individuals yielded yeasts. *D. occidentalis,* another higher altitude species, occurs in rather small numbers at Mather, but too few of this species were analyzed for yeast to draw a conclusion.

TABLE II. Relation between yeast and Drosophila in the Mather area

	D. pseudoobscura ♂	D. persimilis ♂	D. pseudoobscura + D. persimilis ♂♂	D. azteca ♂	D. pinicola	D. occidentalis	Aulacigaster	D. californica	D. miranda	D. busckii	D. subfunebris
No. of flies dissected...	38	17	75	33	55	4	39	1	6	1	2
No. yielding yeast.....	31	16	55	20	31	1	24	1	3	1	1
S. montanus..........	12	2	15	8	3	..	5	..	..	.	..
S. veronae............	2	6	11	3	2	..	10	..	.	.	..
S. cerevisiae var. tetrasporus........	5	3	9	5	4	..	3	1	..	.	..
S. drosophilarum......	3	1	5	2	..	..	5	..	1		..
S. drosophilarum var. acellobiosa........	..	..	..	..	2		.	.	.	..	..
S. florentinus.........	1	..	1		.	..	.	.	..		..
S. pastori............	2	..	2	.			.		.	..	..
S. pini...............	..	..	..	..	..	..	1	..	.	..	..
S. kluyveri..			..	.	1	..	..	..	..	.	..
H. angusta...........	2	..	2	1	2	..	5	..	1	..	..
P. fermentans.........	..	1	1	..	1	..	..	..	..	..	.
P. xylosa...........	..	.	.	..	..	.	..	..	1	..	..
P. membranaefaciens..	..	..	..	..	..	..	1	..	.	..	..
H. valbyensis.........	..	..	..	..	6	..	..	..	..	..	..
H. uvarum...........	1	1	3	..	3	..	..	..	..	..	.
H. osmophila.........	..	1	1	..	2	..	2	..	..		..
Kl. apiculata.........	5	1	6	1	5	..	1	.	..	..	.
Kl. magna...........	3	2	7	2	1	..	2	..	1	..	.
T. stellata............	..	..	..	2	4	..	..	..	..	1	.
T. colliculosa.........	..	..	..	..	..	..	1		.	.	.
Cr. diffluens..........	..	..	..	..	..	..	1	..	..	..	1
Cr. laurentii..........	..	..	..	..	..	..	1	.	.	.	..
Rh. glutinis..........	..	..	..	..	1		.	.			
C. krusei.............	1	1	2	..	2	..	1		.	.	..
C. parapsilosis........	..	..	..	..	1			..	..	.	.
C. mesenterica........	..	..	1	.	..	.	..	.	..	.	..
C. mycoderma........	..	..	..	1	..	..	.	.	..	..	..
C. guilliermondii......	..	..	..	..	..	..	1	..	..	.	..
Candida sp...........	..	..	..	..	..	1	..	..	..	..	..
Tr. fermentans.......	..	..	..	..	1	..	..	..	..	.	..
O. lactis.......	..	1	1	..	.		..	.	.	..	..

Turing to Aspen Valley (Table III) it can be seen that for *D. pinicola,* which is very abundant in this area, only five out of 28 flies yielded yeasts. Of the seven isolates obtained, only 3 are of the fermentative type. It seems possible, therefore, that at Aspen *D. pinicola* feeds on different substrates than at Mather. Most likely these substrates are not rich in the common fermentative yeasts. The fact that *S. veronae* was found in the other two species of Drosophila, indicates that *Saccharomyces* does occur at Aspen Valley,

TABLE III. Relation between yeasts and Drosophila in Aspen Valley

	D. persimilis ♂	D. azteca ♂	D. pinicola	D. occidentalis	D. californica
No. of flies dissected...	3	2	28	21	1
No. of flies cont. yeast..	3	2	5	13	0
S. veronae............	1	..	.	2	..
S. wickerhamii.........	..	..	1	..	..
H. angusta............	2	..	1	4	..
T. pinus..............	..	..	1	..	..
T. glabrata...........	..	..	..	1	..
T. inconspicua........	..	..	1	..	..
C. krusei..............	..	1	..	4	..
C. catenulata..........	..	..	1	5	..
C. parapsilosis.........	..	..	..	1	..
Tr. aculeatum.........	..	..	1	..	..
R. minuta............	..	..	1	..	..

although perhaps not as commonly as at Mather. *D. occidentalis* shows a much higher percentage of individuals carrying yeast, whereas for *D. persimilis* and *D. azteca* the numbers are too small to draw safe conclusions. It might be noted, however, that the yeasts found in the last two species all belong to the main groups of yeast.

At Porcupine Flat (see Table IV) the situation with regard to *D. pinicola* was even more pronounced than at Aspen Valley. Only one out of 18 flies contained yeast, a single species of the non-fermentative genus *Rhodotorula.* None of the common fermentative yeasts were found in *D. pinicola.* This is in striking contrast with *D. persimilis* of which an almost equal number of individuals were dissected, but which had a high percentage of yeast-positive individuals, all of which belonged to *Saccharomyces* or to the other common fermentative yeasts. *D. occidentalis* behaved in this area very much like *D. pinicola,* except that *Saccharomyces montanus* was found in one fly. *D. miranda* appears to have a low percentage of yeast-positive individuals, but the number of flies is too small to draw definite conclusions.

Finally in the Tioga Pass area (see Table V), the distribution of yeasts appears to be in a general way comparable to that described for Porcupine Flat, although the number of flies studied is somewhat too small to be definite on this point.

In addition to the above collections a few flies were studied from other places. Several of the isolations listed in Table I were made from adult flies collected directly from their breeding sites. Thus the six isolations of *Candida parapsilosis* var. *intermedia* were from six adults of *D. occidentalis,* caught at Smoky Jack from *Clavaria* fungi on which they were breeding. Two adults of this species yielded only bacteria. In another case, the same species was found breeding on *Pleurotus* fungi but associated adults were found to be free of yeast. Four individuals of *D. montana,* captured on a breeding site at Yosemite Creek contained either no yeasts at all or *Saccharomyces wickerhamii* nov. sp. (in one adult) and *Cryptococcus diffluens* (in a second adult). Finally, some flies were captured on slime flux of *Abies* in Aspen Valley. A single individual of *D. californica* yielded only bacteria, whereas individuals of *D. pinicola* contained either bacteria only or *T. inconspicua, T. pinus* or *S. wickerhamii* in addition to bacteria (three adults). These results in Aspen Valley are incorporated in Table III. These cases are described in detail by Carson *et al.* 1956 (no. III of this series). In each case the yeasts found in the flies were not found in the breeding sites and vice versa.

TABLE IV. Relation between yeast and Drosophila at Porcupine Flat

	D. persimilis ♂	D. pinicola	D. occidentalis	D. miranda	D. californica
No. of flies dissected	15	18	19	6	1
No. yielding yeasts	9	1	3	1	1
S. montanus	4	..	1	..	..
S. florentinus	1	..	..	..	..
S. dobzhanskii	1	..	..	..	..
S. uvarum	1	..	..	..	..
H. angusta	1	..	..	..	..
K. apiculata	1	..	..	..	..
T. stellata	2	..	..	..	..
Cr. laurentii	..	..	1	..	..
Rh. aurea	..	1	..	..	..
Rh. mucilaginosa	..	..	1	..	..
C. mesenterica	..	..	..	1	1
C. mycoderma	..	..	..	1	..

TABLE V. Relation between yeasts and Drosophila in the Tioga Pass area

	D. persimilis ♂	D. miranda	D. occidentalis	D. pinicola
No. of flies dissected	9	2	12	2
No. of flies yielding yeasts	3	1	3	0
S. veronae	1	..	..	..
K. apiculata	1	..	..	..
T. stellata	..	1	..	..
Cr. diffluens	1	..	1	..
C. mesenterica	1	..	..	..
Tr. aculeatum	..	..	1	..
Pichia sp. (lost)	..	..	1	..

Although complete descriptions of the new species of yeast will be published in a separate article, a brief consideration of the most important or typical yeasts found, seems useful here. Our data confirm those of Shehata *et al.* (1955), showing that *Saccharomyces* is by far the most common genus represented. However, *S. montanus,* our most common species, was not found by Shehata *et al.* It is possible that this organism is not common in southern California where most of Shehata's material was collected. *S. veronae,* a recently described species and originally isolated from grapes in Italy, is apparently very common in California mountains. It was isolated by us at Mather, Aspen Valley and Tioga Pass and by Shehata *et al.* at Jacksonville, Mather, Pinon Flats and Keen Camp. The last two areas are in southern California. *S. drosophilarum* is a new species described by Shehata *et al.*, who found it at Keen Camp and at Mather. Our survey showed this yeast to be common at Mather, but it was not found in the other areas. Another common yeast *S. cerevisiae* var. *tetrasporus* was encountered only in this survey and exclusively at Mather. This form appears very similar to a yeast isolated by Beijerinck in 1898 from the exudate of an oak in Holland and called *S. tetrasporus* by him. Although Lodder and van Rij (1952) included this yeast in *S. cerevisiae,* we believe that there are certain differences, justifying at least a varietal separation. This is a rather important point since several investigators who used live bakers yeast (*S. cerevisiae*) in their traps have isolated this yeast from flies, whereas our studies have convinced us that a typical bakers yeast does not occur in the flies in the mountain areas which we surveyed.

Hansenula angusta was found (combining both surveys) in Jacksonville, Mather, Aspen Valley, Porcupine Flat and Keen Camp and thus appears to be a widespread yeast. According to the present literature it has been isolated only once before from spoiled concentrated Florida orange juice (Wickerham 1951). It appears more likely, however, that its natural habitat is in the forest. Combining the apiculate yeasts in one group (species of *Hanseniaspora* and *Kloeckera*) we have found that these yeasts are very common in the Mather region, but less so at the higher altitudes. Shehata *et al.* found them in southern California and they also appear to be very common in Drosophila in Brazil (Shehata, personal communication). *Candida krusei* is also fairly widespread, since it was found at Mather and Aspen Valley by us and at Pinon Flat and Keen Camp by Shehata *et al.* We have obtained evidence, however, that *C. krusei* may be composed of several varieties. *Candida catenulata* was isolated only at Aspen Valley from *D. occidentalis* and in one case from *D. pinicola.* It is probably limited in its distribution. *Torulopsis stellata* was found at Mather, Porcupine Flat and Tioga Pass but not in southern California by Shehata *et al.* *Saccharomyces dobzhanskii,* a new species described by Shehata *et al.,* was isolated once by these authors at Pinon Flat. Similarly, a single isolate of this species was obtained by us, but in an entirely different life-zone, at Porcupine Flat.

DISCUSSION

In surveying the data obtained, three major variables must be considered, *viz.*, species of yeast, species of Drosophila, and area of collection. Other factors which might influence the relationships between the three major variables are climatic and seasonal changes. The last two factors were found to be negligible in the present study. About half of the yeasts were isolated in 1951 and the other half in 1952 (a few yeasts were isolated in 1954). In both years the collections ranged from early June to late September. All major yeasts were found in both years and in nearly every case they occurred during the whole season from June to September. It should be emphasized, however, that our survey has only qualitative value as to the availability of certain yeasts to Drosophila at different seasons, since the survey is too limited in scope to draw quantitative conclusions in this respect. Moreover, from the standpoint of yeast ecology, the data are indirect. Although the yeasts are found in the crops of Drosophila, there is no reason to believe that they are symbionts (see *e.g.* Shehata and Mrak, 1951). Their true habitat is somewhere in the forest where the flies feed on substrates containing the yeasts. Unless these substrates are known, it is impossible to study quantitatively the availability of certain yeasts in these substrates to a population of flies. Unfortunately, information regarding the natural habitats of the yeasts is still scarce. A thorough study of slime fluxes of *Quercus* and *Abies,* of certain mushrooms and other likely feeding substrates in these areas by Carson *et al.* (1956) showed that these yeast florae are quite different from those in the adult flies. The same results were obtained by Shehata *et al.* (1955), who studied primarily yeasts from *obscura*-group flies and from certain natural substrates in a number of areas in southern and central California.

Since it is exceedingly rare and difficult to find Drosophila in the process of feeding in the areas studied, the knowledge of what yeasts are found in flies may become very important in discovering these feeding places indirectly by a further search for the occurrence of these yeasts in the forest. Shifrine and Phaff (1955) have made a comprehensive study of the yeasts associated with *Dendroctonus* and *Ips* bark beetles and in the phloem galleries which they make. The possibility was considered that the yeasts in these galleries might serve as food for Drosophila. However, virtually no agreement was found between the yeasts from bark beetles, from Drosophila and the slime fluxes and related substrates. The 169 yeasts from bark beetles fell primarily into 4 well-defined major species of yeast, none of which was found in Drosophila or in slime fluxes.

The survey has shown clearly that at least in the Mather area *D. pseudoobscura, D. persimilis, D. azteca, D. pinicola* and flies belonging to *Aulacigaster* feed on substrates that contain essentially similar yeast florae. Whether these substrates are the same for all species cannot be stated with certainty. It is possible, for example, that two different substrates may contain essentially the same types of yeast. In the other areas studied, the number of yeasts and flies examined was much smaller, so that conclusive information is not available. Yet the trend indicates that *obscura*-group flies at the higher altitudes in the mountains have a different diet than *D. pinicola* and *D. occidentalis*.

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Summary

Two hundred and forty-two yeast cultures were isolated from the intestinal tracts of Drosophila collected in the Yosemite Region of California. The most abundant genus was *Saccharomyces,* which was represented by 13 species and 114 isolates. The most common species of yeast were *Saccharomyces montanus* (37), *S. veronae* (30), *S. cerevisiae* var. *tetrasporus* (22), *S. drosophilarum* (15), *Hansenula angusta* (19), *Hanseniaspora valbyensis* (6), *Hanseniaspora uvarum* (6), *Hanseniaspora osmophila* (5), *Kloeckera apiculata* (15), *Kl. magna* (13), *Torulopsis stellata* (10), *Candida krusei* (10), and *C. catenulata* (6). Common bakers yeast (*S. cerevisiae*) apparently does not occur naturally as a food source for Drosophila in the areas studied. In the Mather area, in which most of the flies were collected, *D. persimilis, D. pseudoobscura, D. azteca, D. pinicola* and *Aulacigaster* all contained the same common species of yeasts. At the higher altitudes some evidence was obtained that the *obscura*-group flies tend to feed on the common fermentative yeasts, but *D. pinicola* has other feeding habits. *D. occidentalis* appears to be intermediate in its feeding habits between the other two groups. Five new species and one new variety of yeast were isolated. The most common species of yeasts were found in abundance from early June until late September and occurred both in 1951 and in 1952.

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STUDIES ON THE ECOLOGY OF DROSOPHILA IN THE YOSEMITE REGION OF CALIFORNIA

III. THE YEAST FLORA OF THE NATURAL BREEDING SITES OF SOME SPECIES OF DROSOPHILA

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Introduction

Population genetics, as a study of the causative factors of organic evolution, has scarcely outgrown the theoretical and laboratory stages of its development. In the final analysis, however, it is populations in nature which pose the most perplexing evolutionary problems. Attack on these problems has concerned the ecologist for a century; the geneticist has become involved relatively recently. Flies of the genus *Drosophila* provide unexcelled material for genetic studies, but, as with many other insects, ecological data on natural populations are sparse and qualitative.

This series of studies is concerned with basic ecological information on the Drosophila species of the Yosemite Region of California. Particular attention has been paid to the relations of the flies to the naturally occurring microorganisms, especially yeasts, which form an important ingredient of the natural food of adults and larvae. The present paper is concerned with the yeast flora of the sites of oviposition and larval feeding of some of the Drosophila of the region.

MATERIAL AND METHODS

Breeding sites of Drosophila were located by searching the forest for moist substrates which could support the growth of microorganisms which might in turn be utilized by Drosophila. Substrates with surface moisture available to a small winged insect are scarce in the Sierra Nevada during the dry months of June, July and August when these studies were carried out. This, of course, simplifies the search for breeding sites considerably, because, unlike more mesic areas, many potential sources may be eliminated because of desiccation. Rain water will hydrate previously desiccated substances and render them temporarily available for the feeding but probably not the breeding of Drosophila (*e.g.,* fungi, Carson and Stalker 1951). Such occurrences must nevertheless be exceptional in the Transition and Sonoran zones in the Sierra Nevada during the months of observation, as the normal rainfall for this period is very low.

Two sources of Drosophila food were particularly investigated, namely, fungi and infected sap exudations on trees (slime fluxes). After locating a site, its position was noted but in order to avoid possible contamination, no examinations for the presence of Drosophila were made until after samples for the determination of yeasts had been collected. Following the collection of these samples (see next paragraph) material from the source was removed the searched for eggs, larvae or pupae of Drosophila with a hand lens or low magnification of a wide-field microscope.

Examinations for the presence of yeasts were made by removing bits of material with a sterile loop or scalpel and streaking directly on agar plates. In a few cases, when streaking in the forest was not convenient, the material was collected aseptically in sterile test tubes and plated in the laboratory. For the isolation of yeasts, malt extract agar having a pH of about 4.5 was used. Some bacteria also grew on this medium, but mold contamination was rarely encountered. Duplicate samples were also streaked on plates containing peptone-meat extract agar for the isolation of bacteria. Although several hundred pure cultures of bacteria were collected, identification of this group of microorganisms was not attempted in the present study. The yeasts were obtained in pure culture by conventional plating techniques. All cultures were grown at room temperature (23-25°C). All yeasts showing different gross morphological features on the original streak plate were brought into pure culture. Usually only one or two types of yeast were found on a plate; in rare cases there were three or more. The identifications were done by the system of Lodder and van Rij (1952) and by Wickerham's (1951) procedure for *Hansenula.* Organisms which could not be identified with named species are listed as new species. These will be described in a separate publication (Phaff and Knapp 1956).

OBSERVATIONS

The species of yeast encountered in this study are listed in Table I. The natural sources from which isolations were made, together with the species of Drosophila associated with them are shown in Tables II and III.

TABLE I. Yeasts isolated from slime fluxes and related natural sources. Yosemite Region, Sierra Nevada, California

Name	Number of cultures indentified
Saccharomyces pastori (Guillermond) Lodder et van Rij 1919	12
Saccharomyces elegans Lodder et van Rij 1952	1
Saccharomyces drosophilarum Shehata et al. 1955	1
Hansenula mrakii Wickerman 1951 (imperfect form)	30
Hansenula minuta Wickerham 1951 (imperfect form)	8
Debaryomyces fluxorum nov. spec.*	35
Pichia silvestris nov. spec.*	17
Pichia carsonii nov. spec.*	3
Pichia quercibus nov. spec.*	1
Pichia polymorpha Kloecker 1912	2
Endomyces javanensis Kloecker 1909	3
Candida humicola (Daszewska) Diddens et Lodder 1912	5
Candida mycoderma (Reess) Lodder et van Rij 1870	5
Candida parapsilosis (Ashf.) Lang. et Talice var. *intermedia* van Rij et Verona 1949	1
Trichosporon fermentans Diddens et Lodder 1942	7
Torulopsis inconspicua Lodder et van Rij 1952	1
Cryptococcus laurentii (Kuff.) Skinner var. *magnus* Lodder et van Rij 1952	1
Sporobolomyces roseus Kluyver et van Niel 1924-1925	1
Unidentified	2
Total	136

*These species will be described in a forthcoming paper by Phaff and Knapp (1956).

Of slime fluxes of the California Black Oak (*Quercus kelloggii*) from which yeasts were isolated (Table II) six were proved to be simultaneously serving as breeding sites for Drosophila (third column, Table II). Comparison may be made between the yeast floras of these six and those of the fourteen studied in 1954 in which no Drosophila of any species could be found. There is no apparent correlation between the pres-

TABLE II. Species of Drosophila and yeast present in the slime fluxes of *Quercus kelloggii* near Mather, California. All collections were made in 1954 unless marked (*), in which case they were taken in 1951 or 1952. pp = *Drosophila pseudoobscura* and/or *D. persimilis;* v = *D. victoria;* c = *D. californica;* — = Drosophila was not proved to be present as eggs, larvae or pupae; O = no examination made for the presence of Drosophila

Slime flux Number	BREEDING SPECIES OF DROSOPHILA PRESENT IN:		NUMBER OF CULTURE OF EACH SPECIES OF YEAST IDENTIFIED:														
	1950	1954	*S. pastori*	*S. elegans*	*S. drosophilarum*	*H. mrakii*	*D. fluxorum*	*P. silvestris*	*P. carsonii*	*P. quercibus*	*E. javanensis*	*C. mycoderma*	*C. parapsilosis*	*Tr. fermentans*	*T. inconspicua*	*Cr. laurentii*	Unidentified
3	pp	pp	..	..	..	..	4	..	..	1	..	..	..	..	..	..	..
7	pp;v;c	pp;v	..	..	..	1	1	..	..	..	..	..	..	..	..	..	..
8	pp;v;c	pp	..	..	..	..	9§	..	3	..	3*	4*	..	..	..	..	..
10A	—	pp	..	..	..	8	2	..	..	..	..	..	..	..	..	..	..
33	0	pp	..	..	..	2	1	3	..	..	..	..	..	..	1	..	..
34	0	pp	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..
5B	pp;v;c	—	..	..	..	..	1*	..	..	..	..	..	..	..	..	..	..
17B	pp;v;c	—	..	..	..	1	..	5	..	..	..	..	..	..	..	..	..
5A	—	—	..	..	..	..	2	..	..	..	..	1*	..	..	..	..	..
5C	0	—	..	..	..	7	6	..	..	..	..	..	..	1	..	..	..
10B	—	—	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..
10C	0	—	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..
12B	—	—	..	..	..	4	..	..	..	..	..	..	..	2	..	..	..
20C	0	—	1	..	..	4	..	4	..	..	..	..	..	..	..	..	..
30	0	—	1	..	..	..	..	..	..	..	..	..	..	2	..	..	..
32	0	—	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..
38	0	—	..	..	..	..	2	..	..	..	..	..	..	..	..	..	..
39A	0	—	3	..	..	..	..	..	..	..	..	..	..	2	..	..	..
39B	0	—	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..
41	0	—	3	..	..	..	..	..	..	..	..	..	1	..	..	1	..
42	0	0	1*	..	..	..	..	..	..	..	..	..	..	..	..	..	..
43‡	0	0	..	..	..	1*	..	..	..	..	..	..	..	..	..	..	..
44	0	0	..	..	..	..	2*	..	..	..	..	..	..	..	..	..	..
Other	..	..	..	1	1	1†	..	..	..	..	..	..	..	..	..	..	1
Totals	..	..	11	1	1	31	30	13	3	1	3	5	1	7	1	1	1

§one isolation made in 1952 and 8 in 1954.
†soil sample on which flux from 10A was dripping.
‡located near Groveland, California.

total 110

ence of any particular species of yeast and the presence of young stages of Drosophila in the flux.

Slime fluxes of this particular species of tree appear to be relatively permanent. Thus, of 40 fluxes studied in 1950 (Carson 1951), 22 were little changed in gross appearance four years later; the remainder had dried up. Of the 17 fluxes which were occupied by Drosophila in 1950, three were still being utilized for breeding in 1954. Five new breeding sites, all for *D. pseudoobscura* and/or *D. persimilis* were found in 1954, raising the total known occupied slime fluxes of *Q. kelloggii* in the Mather area to 22 out of a total of 64 examined. As in 1950, *Aulacigaster* sp. was found breeding abundantly in Black Oak slime fluxes but no precise records were kept.

As previously, few adult flies appear to be attracted to the slime fluxes of *Quercus kelloggi.* Flux no. 8 (see Table II and Carson, 1951) was the only one on which adults could be regularly found in 1954 although there were fewer than in 1950. This flux again contained young stages of *D. pseudoobscura* and/or *D. persimilis,* although the presence of the other species found in 1950 (see Table II) could not be demonstrated. No new slime fluxes attractive to adult flies were found in 1954.

Of 240 yeast isolations made from crops of adult Drosophila by Phaff *et al.* (1956; paper no. II of this series), the majority are from the Mather region and a considerable number were taken from *D. pseudoobscura, D. persimilis* and *Aulacigaster* sp. These flies were captured in the immediate vicinity of the trees bearing the slime fluxes which are treated in this paper. The yeast flora of the adult fly crops is nonetheless strikingly different from that of the slime fluxes upon which these species are known to breed in this area.

Although two of the most characteristic yeasts of oak fluxes are also found on the fluxes of *Abies concolor* (Table III), Drosophila does not appear to utilize this site to any appreciable degree, although *Aulacigaster* breeds there abundantly. Despite repeated attempts to find Drosophila larvae in 14 *Abies* fluxes in addition to those from which yeasts were isolated, *osbcura*-group flies were not found. Thus the single case of breeding of *D. pseudoobscura* (out of 46 fluxes examined in 1950) remains unique. A small number of adult *D. pinicola* and an occasional *D. californica* were observed visiting these fluxes in the evening. The crops of such flies, captured as they came to rest on the flux, contained either bacteria only or yeasts which have not been found in *Abies* flux.

TABLE III. Natural sources of yeasts and correlated breeding species of Drosophila. Yosemite Region, Sierra Nevada, California

NATURAL SOURCE			SPECIES OF DROSOPHILA BREEDING THEREON
A. slime fluxes on *Abies concolor*. Aspen Valley, Yosemite; ca. 6400 ft. July, 1954			NONE (in a single instance in 1950, *D. pseudoobscura* was found breeding on *Abies* flux: see Carson 1951)
slime flux no.	yeast	no. of cultures	
3	*D. fluxorum*	1	
	P. silvestris	1	
4	*D. fluxorum*	1	
5	*D. fluxorum*	3	
6	unidentified	1	
7	*P. silvestris*	2	
8	*P. silvestris*	1	
B. *Clavaria* fungi; Smoky Jack, Yosemite. ca. 7200 ft. July 8, 1954			
	Candida humicola	2	*D. occidentalis* *D. pinicola*
C. *Pleurotus* fungi; Aspen Valley, Yosemite. July 17, 1954			
	Candida humicola	3	*D. occidentalis*
D. decaying bark from partially submerged, fallen, dying *Populus tremuloides*. Yosemite Creek, Tioga Road, Yosemite. ca. 7500 ft. July 1954			
	Hansenula minuta	8	*D. montana*
E. rotten log of *Pinus contorta*, Porcupine Flat, Yosemite. ca. 8200 ft. July 1951			
	Pichia polymorpha	1	NONE
F. rotten log, presumably *Abies*. Porcupine Flat, Yosemite. July 1951			
	Pichia polymorpha	1	NONE
G. tunnel of bark beetles in *Abies magnifica*. Tioga Road, Yosemite. ca. 7000 ft. July, 1954			
	Sporobolomyces roseus	1	NONE
	Total cultures	26	

Several other natural sources were investigated and the results are summarized in Table III. Some further details may be of interest. At Smoky Jack campground, *D. occidentalis* was found breeding in decomposing *Clavaria* fungi. A few adult *D. pinicola* were reared from the very same fungi. The crops of adults of *D. occidentalis* caught in the immediate vicinity of the fungi yielded either no yeasts or, from five different individuals, a single species of yeast, *Candida parapsilosis* var. *intermedia* (Phaff *et al.*, no. II of this series). The fungi, however, did not contain this yeast but yielded instead a different species, *Candida humicola*. *C. humicola* was also the only yeast isolated from *Pleurotus* fungi in Aspen Valley. *D. occidentalis* was found breeding in and hovering about these fungi in immense numbers in a low-lying and boggy aspen grove. The site was close to the Aspen Stream collecting station (see Cooper and Dobzhansky, no. I of this series). The density of the population of *D. occidentalis* in this area at this time is indicated by the fact that the routine July collections yielded nearly 16,000 specimens of this species (Cooper and Dobzhansky, no. I of this series). Flies collected directly from the fungi were found to be free of yeast. Despite the care which was taken in these critical instances, no case of the presence of *Candida humicola* in the crops of adult *D. occidentalis* or any other species of Drosophila is known (Phaff *et al.*, no. II of this series).

Only July 8, a breeding site of *Drosophila montana* was located at Yosemite Creek campground on the Tioga Road in Yosemite Park. Several aspens (*Populus tremuloides*) had fallen into a quiet part of the creek. Although they had been submerged earlier in the season, the trees were still green and one had some leaves left. The largest was about eight inches in diameter and just above the point where the trunk emerged from the water was an area of seeping resin. Cracks in the bark around this and in several other places along the trunk, all very near to the water, contained a non-resinous brown slime in which were many freshly laid eggs and young larvae. These were reared and proved to be exclusively *Drosophila montana*. Approximately twelve adult *D. montana* were resting beneath the log, near the cracks. A can of bait, placed near this tree, attracted in a short time a total of 46 *D. montana*, whereas a similar can, approximately 30 feet away, but also at the water's edge, attracted only 5. *D. montana* belongs to the *virilis* species group of the genus and like other members of this group is rarely found except in close proximity to water. The breeding site described here, involving the freshly decaying phloem of a member of the Salicaceae, is strikingly similar to those described by several other authors for other members of this species group (Spieth 1951; Blight and Romano 1953).

Streakings and enrichment cultures made from the above critical material resulted in the obtaining of only a single species of yeast, *Hansenula minuta*. It may furthermore be significant that although a number of platings were made for bacteria, none were obtained from this source. Specimens of *D. montana*, captured from the log by imprisoning them under a vial, containing either no yeasts or *Saccharomyces wickerhamii* (in two adults) and *Cryptococcus diffluens* (in a third adult) but not *H. minuta* (see Phaff *et al.,* no. II).

A feeding site for adult Drosophila was observed not more than 30 feet back from the water's edge near where the breeding site of *D. montana* was located. A small fluxing and actively foaming hole, about 2 mm in diameter, was found near the base of a small willow (*Salix* sp.; diameter about one inch). *D. occidentalis, D. montana* and *D. obscura*-group flies were observed in moderate numbers about this place and all were feeding actively on the material, which was emerging from the small hole in spurts. On the following morning, the same species were observed. Excavation of the hole revealed that it was made by a beetle larva: it extended to the center of the trunk. Beneath the bark, adjacent to the hole, was a small amount of flocculent white material which extended down into the hole; below it was an area of wood frass. No immature stages of Drosophila were present; the place subsequently became completely desiccated and unfortunately, due to circumstances, no yeast samples were taken. Such places, where several species of Drosophila may be observed actively feeding together, are exceedingly difficult to locate.

Discussion

The single most striking fact brought out in the present study is that the yeast flora of the natural sources treated here, many of them known breeding sites for Drosophila, is fundamentally different from the flora found in the crops of adult Drosophila, as reported by Phaff *et al.* (1956) from the same area. Three of the four most common slime flux yeasts (*Hansenula mrakii, Debaryomyces fluxorum* and *Pichia silvestris*) are not known at all from fly crops. The fourth, *Saccharomyces pastori,* was obtained in only two instances from the many hundreds of flies which were dissected. *Candida humicola* (from fungi) and *Hansenula minuta* (from *Populus* bark), although clearly associated with breeding sites, have not been recovered from adult flies, even those captured at the same locations at the same time that the cultures were made. In a few instances, a common "adult food yeast" has been isolated from slime flux. Such cases, however, are so infrequent as to be insignificant. This is especially true as ovipositing females are known to feed, in at least a perfunctory manner, on the materials on which the eggs are deposited and such flies might furthermore contaminate a slime flux with an "adult food yeast" carried on the feet or hypopharynx.

The genus *Saccharomyces* is extraordinarily well represented in fly crops, whereas relatively few isolates of any species of this genus have been made from breeding sites. *Saccharomyces pastori* is an exception, but Phaff and Knapp (1955) have pointed out that the generic position of this yeast is questionable and that it may be more closely allied to *Pichia.* It may be meaningful that the species of *Saccharomyces* and those of several other prominent genera obtained from adult flies are strongly fermentative (*i.e.,* carrying out an active alcoholic fermentation of various sugars) whereas the yeasts considered in this paper (with the exception of the single isolates of *S. elegans* and *S. drosophilarum*) are either weak fermenters of glucose or cannot ferment at all. This includes the *S. pastori* isolates, which are weak fermenters.

In a somewhat similar survey, in which the emphasis was on Southern California, Shehata, Mrak and Phaff (1955) obtained essentially similar results. Prominent yeast from the crops of *obscura*-group flies were rarely encountered in suspected breeding places and the reverse also held. It is also of interest that the bark beetles of pine trees, studied by Shifrine and Phaff (1955), have an entirely specific yeast flora of their own and practically none of these yeasts was found either in Drosophila crops or in slime fluxes of oaks.

That adult and larval food organisms of Drosophila in nature differ has important implications for various experimental procedures in the population genetics of Drosophila. Although Wagner (1944, 1949) utilized strains of yeast from breeding sites for his experiments, the yeasts used by da Cunha (1951) for laboratory population cages were originally isolated from adults. Dudgeon (1954) isolated many yeasts from adult Drosophila and assayed them by measuring the success with which three related species of Drosophila could be reared on them in pure culture. The inadequacy of certain strains, identified only as belonging to the genera *Candida, Torulopsis* and *Saccharomyces,* to support the entire life cycle may reflect the fact that these yeasts were originally isolated from adults rather than from breeding sites.

From the present data, it is not possible to relate the breeding of Drosophila in slime fluxes with the presence of particular yeasts, although *Hansenula mrakii* and *Debaryomyces fluxorum* were the most frequently encountered species. This is perhaps not surprising in view of the obvious great complexity of the microbiological associations in the slime fluxes. No study of the association between Drosophila and bacteria, for instance, has as yet been undertaken, although in connection with the present work many isolations of bacteria were made from slime fluxes and fungi. A considerable number of the fluxes appear to be qualitatively relatively stable and to have some degree of permanence. In such fluxes this probably means that microbiological populations are being maintained in equilibrium. Such equilibrated associations are probably more important in most cases for oviposition than the presence of any specific organism.

The conclusion may be drawn that the known breeding sites are not important as sources of food for adult flies. This is further borne out by direct observation of adults in nature (Carson and Stalker 1951; Carson 1951). The actual whereabouts of feeding sites of adults in nature remains, nevertheless, largely unknown. Several points, however, are now clear. In the first place, it is unlikely that feeding sites consist of large, conspicuous substrates to which large numbers of feeding flies are attracted in the manner that flies are attracted to artificial baits such as fermenting banana mash. The failure of extensive field work in the Yosemite region of California to reveal such places in natural sites is now clearly significant. Secondly, the data of Phaff *et al.* (1956) indicate that the adults of most species of Drosophila and *Aulacigaster* sp. are relatively indiscriminate in their choice of food organisms. Thus, certain abundant "adult food yeasts" are commonly found in several species of flies. Although the adults exhibit distinct preferences in attractivity tests (da Cunha *et al.* 1951; Dobzhansky *et al.* 1956), all species visited all yeasts to some extent. These facts therefore suggest that most species of Drosophila in the Yosemite area share common feeding sites to a considerable extent and that these sites are probably small and ephemeral.

The ecological picture which emerges is one which might be logically expected for a small winged insect with complete metamorphosis and which is adapted to feed on microorganisms. That complete metamorphosis in insects is commonly associated with differences in food habits between adults and larvae is well known. Natural selection, furthermore, would be expected to maintain and extend such divergence in habits because such a result would reduce intraspecific competition between larvae and adults for the same food substances. This would be especially true where an ephemeral source of food suddenly becomes available. Such a source can be exploited only by the winged adult insect which is capable of obtaining food during the few seconds, hours or days that it is available. Such a concept can be applied not only to Drosophila, but to a number of other insects with complete metamorphosis wherein the adults display a similar biological opportunism and thus utilize an often exceedingly transient source of food.

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SUMMARY

1. Yeasts were isolated from natural sources and 134 cultures were identified to species. The majority (110) of the isolations, involving 14 species of yeasts, were made from the slime fluxes of *Quercus kelloggii,* a known breeding site of four species of Drosophila and one of *Aulacigaster.* An imperfect form of *Hansenula mrakii, Debaryomyces fluxorum, Pichia silvestris* and *Saccharomyces pastori* were the most frequently encountered species of yeast.

2. Twenty-five isolations were made from other sources, which in some instances were known to be breeding sites for Drosophila. An imperfect form of *Hansenula minuta* was found associated with a breeding site of *Drosophila montana* and *Candida humicola* with *D. occidentalis* and *D. pinicola.*

3. The yeasts of the breeding sites are strikingly different from these found in the crops of adult flies of the same species from the same region. Larval and adult yeast foods of Drosophila in nature are therefore different and adult flies do not regularly feed from their breeding sites.

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STUDIES ON THE ECOLOGY OF DROSOPHILA IN THE YOSEMITE REGION OF CALIFORNIA

IV. DIFFERENTIAL ATTRACTION OF SPECIES OF DROSOPHILA TO DIFFERENT SPECIES OF YEASTS

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Introduction

It has been shown in the preceding articles of this series that the species of Drosophila which occur in the Yosemite region of California have to some extent subdivided among themselves the habitats available in this region. Each species occurs in a certain range of habitats more commonly than in other habitats. Although this habitat differentiation is relatively slight, it is undoubtedly significant. The present article reports the results of experiments which show that the Drosophila species have become differentiated to some extent also in their behavior; each species is attracted preferentially to food containing a different species of yeast. The existence of different food preferences in different species of Drosophila has been indicated for Brazilian species by the work of Dobzhansky and Pavan (1950), Pavan (1952), and Dobzhansky and da Cunha (1955), and for California species by the exploratory experiments of da Cunha, Dobzhansky, and Sokoloff (1951). The present work is a development and extension of the studies just referred to.

Experimental Techniques

In the exploratory experiments made in the Yosemite region, da Cunha, Dobzansky, and Sokoloff (1951) exposed plastic cups with wads of cotton saturated with suspensions of different pure cultures of yeasts in an odorless nutrient medium. The numbers of Drosophila flies attracted to such suspensions are disappointingly small. In 1952 some exploratory experiments were made by Phaff (unpublished data) using a synthetic agar medium on the bottom of tin cans, about the size of a plastic cup, in which the test yeast was actually growing. This bait also attracted rather small numbers of flies. In their experiments made in Brazil, Dobzhansky and da Cunha (1955) used a bait consisting of autoclaved banana inoculated with a desired species of yeast. Autoclaved banana without yeast attracts few or no Drosophila, but fermenting banana is a potent attractant. The attractivity of a bait is a function of the fermenting microorganism as well as of the fermented substance and the surface area exposed; it is not unlikely that the yeast used would evoke different reactions in the flies if combined with a fermentable medium other than banana.

As stated in the first paper of this series (Cooper and Dobzhansky 1956), the bait was placed in 6 x 8 inch cans with friction tops. The bait was always used between the third and seventh day after inoculation to minimize the effect of age of the bait. The cans were exposed in fixed locations. The distances between the neighboring cans were of the order of 10 to 20 meters, so that the neighboring cans competed with each other for the flies which they attracted. In all, 15 different species of yeasts have been used; the names of these yeasts and the sources from which they were originally isolated are shown in Table I. All but two of the yeasts were isolated from the crops of Drosophila flies in the same region in which the present experiments were made. One yeast (*Saccharomyces elegans* No. S-16) came from a slime flux (#8) on an oak tree which attracted flies, and one (*Saccharomycodes ludwigii* No. 114) is from an unknown source. The last species has been reported to occur in oak exudate in Europe and in grape must (Lodder and van Rij 1952). Two kinds of experiments were done. In one kind, 18 baited cans were exposed, inoculated with 6 different yeasts as shown in Table II; here, then, each of the 6 yeasts was represented by 3 cans. In the second round of experiments, 18 cans were used baited with 9 different yeasts, as shown in Table III; each of the 9 yeasts was, consequently, represented by 2 cans. One of the yeasts (No. 310, *Kloeckera apiculata*) was used in all experiments, and served as a common denominator to make the experiments comparable.

TABLE I. Yeasts used in the experiments

Isolate Number	Taxonomic Designation	Source
114	*Saccharomycodes ludwigii* Hansen 1889	C.B.S. (Holland) culture collection (isolation source unknown)
237	*Torulopsis stellata* (Kroemer et Krumbholz) Lodder 1931	*D. pinicola*, Mather
334B	*Hanseniaspora osmophila* (Niehaus) *nov. comb.* 1932	*Aulacigaster*, Mather
311A	*Saccharomyces montanus* nov. sp.*	*D. azteca*, Mather
123B	*Saccharomyces montanus* nov. sp.	*D. persimilis*, Porcupine Flat
36A	*Candida krusei* (Cast.) Berkhout 1910	*D. occidentalis*, Aspen Valley
S-16	*Saccharomyces elegans* Lodder et van Rij 1952	*Quercus kellogii* (No. 8), Mather
246A	*Hanseniaspora valbyensis* Klöcker 1912	*D. pinicola*, Mather
310	*Kloeckera apiculata* (Reess *emend.* Klöcker) Janke 1870	*D. pseudoobscura*, Mather
303	*Saccharomyces cerevisiae* Hansen var. *tetrasporus* (Beijerinck) Dekker *nov. comb.*	*D. persimilis*, Mather
18B	*Hansenula angusta* Wickerham 1951	*D. pseudoobscura*, Mather
367B	*Saccharomyces veronae* Lodder et van Rij 1952	*D. persimilis*, Mather
42A	*Candida catenulata* Diddens et Lodder 1942	*D. occidentalis*, Aspen Valley
12C	*Saccharomyces drosophilarum* Shehata et al. 1955	*D. azteca*, Mather

*Latin description to be published in Antonie van Leeuwenhoek.

As shown by Dobzhansky and Pavan (1950) and repeatedly confirmed since then, the absolute and relative numbers of flies of different species attending a bait depend not only upon the nature of the bait but also upon the microenvironment in which the bait is exposed. Baits exposed as close as 10 meters apart may attract different proportions of visitors. The purpose of our experiments was to test the attractivity of the baits; consequently, the disturbing effects of the different concentrations of flies in different microenvironments had to be minimized or eliminated. Following Dobzhansky and da Cunha (1955), we exposed the same series of baits on several successive days, rotating the positions of the baits so that each yeast used as bait was exposed in each position (in the experiments in which 6 baits were used), or at least in each second position (in the experiments in which 9 baits were used). The flies visiting each bait were collected at intervals with the aid of collecting nets, were placed in separate vials, and their species were classified. The number of the flies of a given species found on each bait was then expressed as the pecentage of the total number of individuals of that species caught on the 6 (or 9) baits of a series. The numbers reported in Tables II and III represent, then, the mean percentages of the flies of certain species which came to different baits on different days of collecting, when these baits stood in different positions.

This method has the obvious drawback that the basic datum used, the percentage of flies of a given species on a given yeast of a given series on a given day, may be derived from different numbers of the flies caught. These numbers are obviously greater for common than for rare species, and greater under favorable collecting conditions (warm evenings) than under unfavorable ones (cool mornings). We have arbitrarily set the minimum number of the flies of a given species on all baits of a series from which the percentages can be calculated as 10. When fewer flies were caught, adjacent series of baits (6 or 9 baits in the two kinds of experiments) were combined, to make the total number of individuals of a given species 10 or more. This explains why the numbers of "series" (the rightmost column in Tables II and III) are different for different species. The magnitude of the standard error of the mean percentage depends, of course, on the number of these "series." For more details concerning the methods of the treatment of the data, see Dobzhansky and da Cunha (1955).

THE SIX-YEAST SERIES

Table II reports the data for the experiments in which six baits with different yeasts were exposed. Since females of *Drosophila pseudoobscura, D. persimilis,* and *D. azteca* cannot be easily distinguished, they have been disregarded; the males of *D. azteca* are distinguishable and are treated separately from the "*obscura* group ♂♂," which is a designation combining the two other species, *D. pseudoobscura* and *D. persimilis*. In *D. pinicola* the numbers of males caught were much smaller than the capture of females (see Cooper and Dobzhansky, the first paper of the present series); some of the series of experiments for this species, and also for *D. occidentalis* are

Table II. Percentages of flies of a given species which visited each of the six different yeasts. M = Mather, A = Aspen

Species	Place and Time	303	18B	367B	42A	12C	310	Flies counted	Series
D. obscura ♂♂	M, June I	14.3	3.6	19.1	3.5	26.6	33.0	659	20
"	M, June II	13.8	4.8	9.8	4.3	23.6	43.8	438	10
"	A, June	12.3	6.7	21.7	5.4	12.7	41.3	619	15
"	M, Aug. I	19.0	5.2	13.7	9.8	21.7	30.7	676	22
"	M, Aug. II	17.1	5.9	21.7	4.2	22.6	28.6	571	20
"	A, Aug.	18.3	3.3	19.4	16.4	14.6	28.0	336	12
"	Mean	16.0	5.0	17.9	7.0	20.8	33.3	3299	99
"	Error ±	1.00	0.50	1.10	0.86	1.22	1.56		
D. azteca ♂♂	M, June I	21.8	8.8	18.8	6.2	16.8	27.9	591	17
"	M, June II	15.9	5.7	20.7	6.3	22.3	29.1	324	9
"	A, June	11.6	3.8	19.2	3.8	30.8	30.8	26	1
"	M, Aug. I	28.6	5.4	16.8	11.7	19.7	18.0	1660	21
"	M, Aug. II	27.8	6.5	17.7	3.7	24.1	20.4	1308	20
"	A, Aug.	20.6	11.1	18.4	16.6	9.3	23.4	139	8
"	Mean	24.3	7.1	18.1	8.1	19.5	22.9	4048	76
"	Error ±	1.47	1.00	1.24	1.13	1.43	1.63		
D. occidentalis	M, June I	21.8	3.4	26.6	4.5	21.4	22.4	709	18
"	M, June II	15.7	3.7	13.4	4.0	34.3	29.0	272	7
"	A, June	17.7	5.6	23.0	6.0	28.6	18.9	1729	18
" ♀♀	M, Aug. I	13.8	5.7	10.1	9.6	39.3	21.6	99	7
" ♂♂	M, Aug. I	17.7	1.7	11.7	14.0	35.5	19.5	112	6
" ♀♀	M, Aug. II	21.0	4.8	23.8	5.2	24.5	21.0	118	7
" ♂♂	M, Aug. II	15.7	4.0	26.7	0.9	36.0	16.7	105	6
" ♀♀ & ♂♂	A, Aug.	20.1	8.8	15.5	7.1	26.0	22.4	2680	10
" ♀♀ & ♂♂	Mean	18.5	4.8	20.4	6.0	28.9	21.4	5824	79
" ♀♀ & ♂♂	Error ±	1.51	0.62	1.61	0.98	1.69	1.52		
D. pinicola	M, June I	19.8	8.7	23.1	5.5	27.9	14.5	952	18
"	M, June II	13.7	10.9	9.7	4.2	34.7	27.3	356	9
"	A, June	17.9	9.7	22.6	5.2	27.6	17.0	4967	18
" ♀♀	M, Aug. I	12.8	10.4	16.7	8.7	27.3	24.4	233	10
" ♂♂	M, Aug. I	4.3	11.3	18.3	13.3	28.3	27.0	40	3
" ♀♀	M, Aug. II	16.5	9.3	14.1	3.0	32.9	24.1	306	15
" ♂♂	M, Aug. II	26.5	3.5	16.5	3.5	35.5	14.5	32	2
" ♀♀	A, Aug.	15.2	13.2	22.8	8.1	26.6	18.1	1041	15
" ♂♂	A, Aug.	15.8	7.5	21.4	12.1	23.2	19.6	569	10
" ♀♀ & ♂♂	Mean	16.3	9.9	19.3	6.5	28.1	20.0	8496	100
" ♀♀ & ♂♂	Error ±	0.90	0.77	1.00	0.84	1.32	1.12		
Aulacigaster sp.	M, June	12.7	9.7	22.1	26.0	12.9	16.6	115	7
"	M, Aug.	22.7	10.7	17.5	21.6	12.0	15.1	134	11
"	Aspen	14.8	8.5	23.8	25.3	10.3	16.3	88	6
"	Mean	17.8	9.9	20.5	23.8	12.0	15.8	337	24
"	Error ±	3.15	2.06	2.85	3.06	2.00	2.15		
D. miranda	Mean	16.1	3.8	15.4	8.7	27.0	28.8	1400	43
"	Error ±	1.55	1.03	1.89	1.68	2.15	2.30		
D. melanogaster	Mean	11.6	6.1	8.6	1.8	37.6	34.9	488	16
"	Error ±	2.69	2.08	1.60	0.85	4.95	4.21		
D. californica	Mean	3.1	3.5	23.5	11.3	12.5	45.5	159	11
"	Error ±	1.12	1.63	5.19	2.59	3.84	7.03		
D. immigrans	Mean	33.3	33.3	13.3	6.7	6.7	6.7	15	1
D. victoria	Mean	25.0	0	33.3	16.7	8.3	16.7	12	1

listed separately in Table II for females and for males. No significant differences in the attractivity of the baits used for the two sexes emerge, however, from the data.

Supposing that the six baits are equally attractive to the flies of a given species, the numbers of the flies attending these baits should be equal within the limits of the sampling errors (16.7 percent on each bait). Table II shows that this is not so. The *obscura*-group males are attracted most strongly to yeast No. 310 (33.3 ± 1.56%), yeast Nos. 12C, 367B, and 303) are less attractive, and Nos. 42A and 18B are least attractive.

D. azteca reacts to the yeast differently from the *obscura* group of species. Here the yeasts Nos. 303 and 310 are equally attractive, and Nos. 12C and 367B only slightly less so. *D. occidentalis* shows a still different attractivity pattern, the yeast No. 12C being most attractive, and Nos. 310, 367B and 303 being equivalent. *D. pinicola* behaves like *D. occidentalis*. Among the less frequent species, *Aulacigaster* is attracted most strongly to No. 42A, which is a yeast which the Drosophila species in the Yosemite region seem to dislike. *D. californica* is most partial to No. 310, and *D. melanogaster* for Nos. 12C and 310. *D. immigrans* and *D. victoria* are too rare to make the conclusion safe, but the data indicate preference patterns quite different from the other species.

The possibility has been considered that a preference of files for a given species of yeast may change as this yeast becomes more or less common in the environment. Table II shows that the experiments were done in two different localities with rather different vegetations (Mather and Aspen, see the first paper of the present series) and on different months, from early June (June I = June 1st-7th, June II = June 15th-20th), to late August (August II = August 20th-27th). Although the figures are variable, there is no indication of systematic changes in the attractivity of the different yeasts in space or in time within the limits studied.

THE NINE-YEAST SERIES

The results of the experiments in which nine different yeasts were used are reported in Table III. On the basis of equal attractivity, 11.1% of the flies should be found on each bait. The species of Drosophila again show different preference patterns. Males of the *obscura* group prefer the baits with the yeasts Nos. 237, 246A, 310, 334B and 114 to the other four yeasts. The *azteca* males are partial to No. 246A, and somewhat less so to Nos. 237, and 334B. *D. occidentalis* prefers No. 237, and No. S-16 is the second on the preference list. *D. pinicola* also has a decided preference for No. 237 but does not seem to discriminate between Nos. S-16 and 123B. *D. miranda*, which is a member of the *osbcura* group of species, has a different gamut of preferences from *D. pseudoobscura* or *D. persimlis*. *Aulacigaster* and *D. californica* are strongly partial to No. 237. No consistent differences in the preference patterns on different months and in the two localities (Mather and Aspen) are apparent.

Da Cunha, Dobzhansky, and Sokoloff (1951) observed that the yeast isolated from a given species of Drosophila was attractive to the species from which it was isolated more than to other species. Our more abundant material fails to confirm this relationship, as a comparison of the data in Table I with those in Tables II and III will easily show. This is not surprising since the observations on the crop contents of Drosophila in the Yosemite region (see the second paper of the present series) have shown that many species of yeasts occur in each species of Drosophila.

THE SIBLING SPECIES, DROSOPHILA PSEUDOOBSCURA AND DROSOPHILA PERSIMILIS

These two species can be classified only by breeding tests or by examination of the male genitalia (see the first paper of the series). Most of the males attracted to the baits were classified by genitalic examination. The results, reported in Table IV, are disappointing inasmuch as they fail to reveal any differences between these species in the yeast preferences.

A behavioral difference between these species has neverthless been found. Dobzhansky (1951) recorded that among the flies which attend the yeasted baits in the morning the proportion of *D. pseudoobscura* is lower, and that of *D. persimilis* is higher, than among the flies attracted during the evening period of activity. We can confirm this finding on the present abundant material. The number of males of *D. pseudoobscura* and *D. persimilis* in the morning and evening catches in June, July, and August 1954 were as follows (classified by inspecton of the genitalic armatures):

Month	Morning		Evening	
	pseudo-obscura	*per-similis*	*pseudo-obscura*	*per-similis*
June	68	111	682	432
July	210	297	694	446
August	65	75	681	443

DISCUSSION AND SUMMARY

Evidence is presented in the present series of four articles on the ecology of Drosophila in the

Yosemite region which shows that (1) fourteen species of this genus occur in the region, (2) each species occupies a certain range of habitats, (3) the habitat ranges of the different species overlap, (4) a variety of species of microorganisms which serve at least as a part of the food supply for Drosophila exist in the same region, (5) the microorganisms found in the alimentary canal of adult Drosophila are as a rule different from those found in the slime fluxes and in other places where Drosophila larvae are known to occur, (6) each species of Drosophila has behavioral mechanisms which cause it to be attracted preferentially to different species of yeasts, although (7) all the yeasts tested attract all Drosophila species to some extent.

Table III. Percentages of flies of a given species which visited each of the nine different yeasts. M = Mather, A = Aspen

Species	Place and time	114	237	334B	311A	36A	123B	S-16	246A	310	Flies counted	Series
D. obscura ♂♂	M, July I...	11.5	11.9	16.9	8.1	4.4	8.8	9.2	17.9	11.7	1045	18
"	M, July II..	14.6	20.9	8.4	10.7	3.7	8.8	6.9	13.6	12.6	187	15
"	A, July.....	9.8	21.1	12.7	6.0	6.0	5.8	7.8	13.8	16.6	730	10
"	M, Sept....	10.5	16.3	13.1	6.3	8.0	6.1	7.3	14.9	17.8	1313	15
"	Mean......	11.7	16.9	13.0	7.9	5.4	7.6	7.8	15.3	14.4	3275	58
"	Error ±....	1.03	1.45	1.24	1.00	0.72	0.79	0.77	1.27	1.25		
D. azteca ♂♂	M, July I...	10.6	9.8	17.7	6.6	2.9	6.9	9.7	26.2	9.2	1109	18
"	M, July II..	13.0	16.2	11.1	6.3	3.7	6.1	8.0	23.5	10.9	1243	16
"	A, July.....	3.6	30.0	16.9	2.9	2.6	8.6	9.4	14.9	11.1	230	7
"	M, Sept....	5.3	19.6	13.8	10.3	6.4	8.3	5.8	22.3	8.3	2174	16
"	Mean......	8.9	16.8	14.6	7.1	4.1	7.3	8.1	23.0	9.7	4756	57
"	Error ±....	1.15	1.60	1.51	0.93	0.73	1.03	0.95	1.72	1.19		
D. occidentalis												
" ♀♀	M, July I...	9.4	18.0	14.0	14.1	5.2	11.3	10.5	10.6	6.8	167	11
" ♂♂	M, July I...	14.6	24.9	13.2	9.3	3.5	10.3	11.8	9.0	3.5	165	10
" ♀♀	M, July II..	11.8	31.8	3.2	9.3	1.4	10.9	19.2	6.6	6.6	191	11
" ♂♂	M, July II..	6.2	29.9	5.3	9.1	3.4	10.9	22.8	7.7	4.9	163	10
" ♂♂ & ♀♀	A, July.....	6.5	30.9	11.8	6.5	4.4	6.5	15.8	7.7	10.3	15888	12
" ♀♀	M, Sept....	7.8	24.5	8.5	7.1	8.9	9.1	11.4	12.8	10.6	149	8
" ♂♂	M, Sept....	5.8	23.6	6.9	9.1	9.1	7.4	12.3	16.4	9.3	137	8
" ♂♂ & ♀♀	Mean......	9.0	26.5	9.1	9.3	4.8	9.5	15.0	9.7	7.3	16860	70
" ♂♂ & ♀♀	Error ±....	0.81	1.52	0.89	0.89	0.70	0.84	1.28	1.13	0.92		
D. pinicola ♀♀	M, July I...	17.8	20.8	9.9	4.6	0.3	8.4	13.1	11.9	13.1	205	9
" ♂♂	M, July I...	9.0	31.5	4.0	5.0	0	0	28.5	9.0	12.5	22	2
" ♀♀	A, July.....	6.8	27.2	8.0	8.7	5.3	12.0	13.7	8.6	9.8	2110	12
" ♂♂	A, July.....	7.8	42.3	8.1	4.6	3.4	10.9	7.8	5.9	8.6	480	10
" ♀♀	M, July II..	14.8	23.3	7.3	8.5	1.2	13.2	14.8	11.7	4.8	101	6
" ♂♂	M, July II..	14.0	49.0	7.5	0	0	7.5	14.0	4.0	4.0	28	2
" ♀♀	M, Sept....	6.0	25.0	11.5	8.8	2.5	18.0	10.5	8.2	9.2	198	13
" ♂♂	M, Sept....	5.3	36.8	7.8	1.5	8.5	6.0	16.3	11.3	6.3	53	4
" ♀♀ & ♂♂	Mean......	9.6	29.6	8.8	6.4	3.0	11.7	12.7	8.9	9.1	2765	58
" ♀♀ & ♂♂	Error ±....	0.96	1.84	1.09	0.77	0.57	1.07	1.33	0.96	1.01		
Aulacigaster sp.	M, July I...	5.3	37.6	15.3	1.4	11.0	4.0	14.6	3.1	8.6	89	7
"	M, July II..	7.8	45.0	1.6	3.6	13.4	2.0	13.6	2.0	11.2	79	5
"	M, Sept....	5.4	26.4	9.7	16.0	15.0	4.1	4.0	6.9	12.1	133	7
" ♀♀ & ♂♂	Mean......	6.0	35.4	9.6	7.4	13.1	3.5	10.4	4.2	10.6	301	19
" ♀♀ & ♂♂	Error ±....	1.74	4.60	2.35	2.05	3.21	0.93	2.16	1.26	1.39		
D. miranda	Mean......	11.0	17.2	12.8	10.3	5.7	10.1	10.9	10.7	11.7	608	23
"	Error ±....	1.89	3.15	2.21	2.32	1.30	1.79	1.98	1.85	2.51		
D. melanogaster	Mean......	11.1	7.8	12.8	12.9	4.3	12.2	7.1	14.9	17.3	2927	20
"	Error ±....	2.09	1.18	1.18	2.39	0.91	1.86	1.11	1.41	2.02		
D. californica	Mean......	6.6	47.9	9.4	2.4	2.6	2.1	12.6	1.0	15.6	89	7
"	Error ±....	3.52	10.60	4.48	1.56	1.64	1.36	5.24	1.00	6.84		
D. immigrans	Mean......	14.3	14.3	21.4	0	14.3	7.1	0	21.4	7.1	14	1
D. victoria	Mean......	8.3	16.6	11.1	8.3	13.9	2.8	8.3	19.4	11.1	36	1

The above findings fit together in a self-consistent pattern. Drosophila flies which inhabit a given region form a community which possesses an interesting organization. The community subsists by utilizing the surplus production of yeasts and other microorganisms, which in turn exploit the fluxes and other by-products of vegetation which are rich in carbohydrates. Owing to long-continued natural selection, the Drosophila community has become differentiated in such ways which minimize the competition between the members of the community. Every species of Drosophila has its own dietary preferences, as well as its own altitudinal and habitat range. At the same time, no species is overspecialized to a point where it would become monophagous and could be endangered by the vagaries of the environment. An example of this is the observation that *D. pinicola* at Mather contains yeasts in the majority of cases, but at Aspen Valley and other higher locations the crop contents consist primarily of bacteria (see the second paper of this series). All Drosophila seem to be able to feed on all yeasts. This statement is not contradicted by the findings of Wagner (1944, 1949) and of Dudgeon (1954) that some species of Drosophila are unable to develop on pure cultures of some microorganisms. In the natural habits the diet of the flies is probably always varied and provides them with all the nutritional essentials for successful development. Whether the yeasts to which a given species of Drosophila is preferentially attracted are the ones which are nutritionally most favorable for them remains to be determined.

TABLE IV. Percentages, with standard errors, of *Drosophila pseudoobscura* and *Drosophila persimilis* males which visited the different yeasts

Yeast	Pseudoobscura	Persimilis	Yeast	Pseudoobscura	Persimilis
114......	12.5±1.26	11.5±1.44	303.....	16.5±1.17	15.6±1.29
237......	17.5±1.48	18.9±1.79	18B.....	6.7±0.81	3.7±0.61
334B.....	12.8±1.55	11.3±1.44	367B....	18.3±1.20	17.8±1.11
311A.....	8.9±1.49	8.0±1.26	42A.....	7.8±1.11	6.9±0.89
36A......	4.7±0.92	6.2±1.00	12C.....	20.2±1.39	21.4±1.51
123B.....	5.9±0.98	7.9±1.00	310.....	30.3±1.35	34.6±1.91
S-16.....	8.6±1.05	6.9±0.99			
246-A....	15.3±1.60	14.8±1.41			
310......	13.5±1.18	14.5±1.59			

The finding that the yeasts in the crops of adult flies are not the same as those found in the slime fluxes and fungi which furnish at least a part of the larval food creates a puzzling problem. We are entirely in the dark concerning the main sources of food on which adult Drosophila chiefly feed. It is, however, interesting to know that natural selection has acted to minimize the competition for food not only between different species of Drosophila but also between the different stages of the life cycle of the same species, between larvae and adults. Those who breed Drosophila in laboratory cultures know that the flies deposit only few or no eggs on culture medium which contains many larvae. In experimental "population cages" it can easily be observed that the adults feed chiefly on the cuture medium with few or no larvae and avoid the medium which contains larvae. Nevertheless, the adult will not starve to death if it is offered only a food with larvae. The situation is here probably the same as with the preferences for the different yeasts in the banana medium; when a choice is available it is exercised, but if there is no choice any yeast can serve as food.

Approximately 33,000 Drosophila adults, belonging to non-domestic species, were captured and identified at the Mather Station during June, July and August, 1954. This represents only about 20-30 grams wet weight of flies, a rather small biomass. Based on data given by Sang, McDonald and Gordon (1949), it may be roughly estimated that it requires about one gram (dry weight) of yeast to raise one gram (wet) of *Drosophila melanogaster* adults (about 2000 flies). On this basis, the entire biomass collected at Mather during 1955 could have been reared in the laboratory on an amount of pure yeast equal to less than the contents of four packages of commercial dry active yeast. This conclusion is in line with the observation of Spencer (1950) who reared 4084 *D. hydei* from a single quarter-pint bottle containing a mixture (about 25 cc) of baker's yeast and raw oatmeal. The concentration of yeast in the natural breeding sites of Drosophila is unknown, but even if the above calculation is half or twice the actual condition, the order of magnitude is such that no very great quantity of source material is required to explain the size of the populations of Drosophila at Mather. On the above basis, the breeding sites now known (slime fluxes and fungi) seem to be fully adequate sources of the observed populations in this region.

In conclusion, it may be pointed out that a comparison of the Drosophila-yeast relationships in different regions may be of considerable interest. The Drosophila community in the Yosemite region contains a relatively small number of species (it should be kept in mind in this connection that four of the species recorded in the region, namely *D. melanogaster, D. immigrans, D. busckii,* and *D. hydei,* are species associated with man and do not belong to the "natural" community). Greater numbers of species of

Drosophila are found in many other regions, especially in the tropics, and the variety of microorganisms and of substrates may also be greater. Theoretically, we may expect that the specialization of food preferences will be pushed farther in communities in which the variety of foods and of consumers is greater than in communities where the variety is less. The exploratory study of Dobzhansky and da Cunha (1955) of the Drosophila-yeasts relationships in some parts of Brazil gave indication that this expectation may be realized, but more data are needed to make this conclusion secure.

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A TRACER STUDY OF THE PHOSPHORUS CYCLE IN LAKE WATER[1]

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Introduction

The phosphorus cycle in lakes has long been of interest to limnologists because available phosphorus has been thought to be a limiting factor in the production of algae and hence of fish in many lakes. Before radioactive phosphorus became available, what information there was about the circulation of phosphorus came from measurements of temporal changes or vertical differences in concentration of inorganic phosphate or organic phosphorus under natural conditions or after addition of large quantities of fertilizer containing available phosphorus. But these methods were inadequate and only with the introduction of radioactive tracer techniques did it become possible to study the rate and mechanism of phosphate circulation directly.

More definite information about the mechanism by which phosphate is removed from the trophogenic zone has now been obtained by several workers who have added radioactive phosphate ($P^{32}O_4$) to the surface of small lakes. It is known that inorganic phosphate is fairly quickly removed from solution in the epilimnion because a loss of P^{32} from solution (*i.e.* from filtered or Foerst-centrifuged water) has been demonstrated by Coffin *et al.* (1949), Hutchinson and Bowen (1950), Hayes *et al.* (1952) and Whittaker (1953). Hayes demonstrated that the loss of P^{32} from solution could be explained by postulating a turnover of inorganic phosphate with the phosphate of 'lake solids' but did not show which fraction of the solids was most active in causing this turnover. However, it appears from the work of Hutchinson and Bowen, and Whittaker that plankton is primarily responsible. Following the uptake of inorganic phosphate by plankton there is a transfer of phosphorus to the hypolimnion, presumably by sedimentation of plankton, and a subsequent release of soluble, inorganic phosphate in the hypolimnion (Hutchinson and Bowen 1950).

There is still some doubt as to whether there is a loss of P^{32} from the open water. The only figures on the amount of P^{32} remaining in the open water indicated that there was almost no loss (Hutchinson and Bowen 1950), but these workers as well as Coffin *et al.* (1949) found P^{32} in rooted aquatic plants and Hayes *et al.* (1952) found an uptake of P^{32} in bottom deposits.

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Although tracer studies have shown that plankton take up P^{32} rapidly, no attempt had been made to fractionate the plankton to show which organisms are most active in this process. That planktonic algae take up and utilize inorganic phosphate for growth is beyond question. However, it is also known that when natural waters are stored, there is a large increase in the bacterial population and a loss of dissolved phosphate (Waksman *et al.* 1937; Renn 1937). Although it may be inferred from these results that bacteria might also take up phosphate under natural conditions, this possibility has received little attention, probably because the rapid multiplication of planktonic bacteria has been thought to be peculiar to stored water.

The present paper describes the results of a tracer experiment which give additional information about the circulation of phosphate in a small lake, particularly the removal of phosphorus from the open water by littoral organisms and bottom deposits. It is also shown that the turnover time of dissolved inorganic phosphate is much shorter than had been previously supposed (minutes instead of days) and that bacteria are largely responsible for causing this turnover.

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METHODS

Radioactive phosphorus (P^{32}) was used as a tracer to demonstrate the movements of naturally occurring phosphorus. Carrier-free P^{32} was obtained from Atomic Energy of Canada Limited as phosphate dissolved in .005 N hydrochloric acid. Radioactivity was measured with a shielded, end-window, Geiger-Müller tube which had a background of 15-20 c.p.m (counts per minute) and a counting efficiency of approximately 15% for P^{32} under the conditions used. Whenever possible, the time for 5,000-10,000 counts was measured. All measurements were corrected for radioactive decay and for variations in counter efficiency but corrections were not applied for self-absorption of radiations. Samples in which radioactivity was to be determined were spread evenly over the bottom of flat aluminum trays, one and one-eighth inch in diameter with a rim one-eighth of an inch high. In order to prevent concentration around the rim and to ensure even distribution of the dry residue from liquid samples, a disc of filter paper slightly smaller than the tray diameter was placed in the tray prior to addition of the sample.

Inorganic phosphate was determined by the ammonium molybdate-stannous chloride method. Four milliliters of 2.5% ammonium molybdate in 10 N sulphuric acid and 0.5 ml of a 0.2% solution of potassium chlorate were added to duplicate, 100-ml samples. Then 0.3 ml of a 1.3% solution of stannous chloride in 0.3 N hydrochloric acid was added and the color which developed in 25 min. was measured in a Lumetron colorimeter made by the Photovolt Corporation, N. Y. A 650 mμ filter and a 150-mm light path were used. All glassware was soaked in dilute nitric acid between analyses. Total phosphorus was measured by the method of O'Reilly and Papson (Manuscript).

The method of distributing P^{32} over Toussaint Lake was essentially the same as that used by earlier workers. The sample of radioactive phosphorus (200 millicuries) was diluted with 20 liters of distilled water containing five grams of potassium dihydrogen phosphate which was added to prevent adsorption of P^{32} on the glass container and was slowly siphoned into the water from a moving boat. The addition of tracer took over three hours, during which time the lake was circled and crossed many times in order that the tracer would be distributed as evenly as possible.

Samples of water for measurement of radioactivity and for chemical determinations were taken at meter intervals with a one-liter Friedinger water bottle. Two stations were sampled (Fig. 1), one at the deepest part of the lake and the other near weed beds at the east end where the depth was five meters. Water temperatures were measured with a thermistor thermometer similar to that described by Mortimer and Moore (1953) and dissolved oxygen was measured by the unmodified Winkler method. Bottom sediments were collected with a sampler built at the Ont. Fish. Res. Lab. The sampler is essentially a transparent, plastic cylinder one inch in diameter and one foot long with a hinged valve at the top end. The valve allows water to leave the cylinder while it is being lowered into the mud and prevents water from entering the cylinder while it is being pulled out of the mud. As a precaution against loss of mud, the bottom end is closed by means of a spring-loaded cup as soon as the sampler is withdrawn from the mud. Only the samples in which

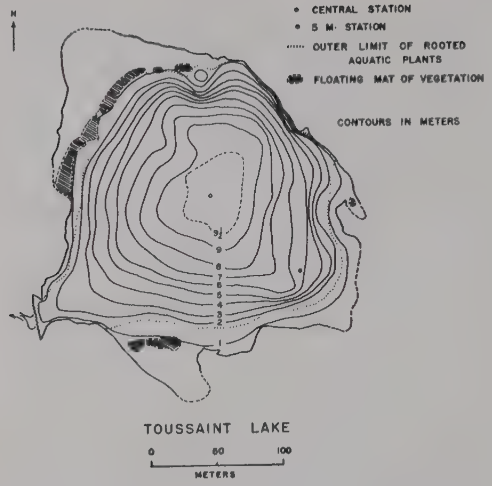

FIG. 1. Contour map of Toussaint Lake showing sampling stations used in tracer experiment.

the surface mud was undisturbed and the water above it perfectly clear were used for determination of radioactivity.

Radioactivity of water and plankton was measured separately. The plankton was separated from one liter of water by means of a Foerst centrifuge, plated directly on a counting tray and dried under a heat lamp. Water samples were acidified in beakers with a few drops of nitric acid, concentrated to about four milliliters and transferred to counting trays for final drying. Beakers were covered with watch glasses and, after the sample was removed, were fumed out with a few ml of dilute nitric acid which was then added to the sample. This method of concentrating the water samples gave better than 95% recovery of P^{32}.

The top quarter-inch of mud was used for measurement of P^{32}. Mud samples from deeper water were plated directly on a counting tray and dried. Mud samples from shallow water contained a large proportion of sand and were therefore extracted for one hour with boiling nitric acid (70%), diluted and filtered. The filtrate was concentrated, plated on a counting tray and dried. This method extracted 90-95% of the P^{32} and considerably reduced the self absorption of the sample.

Bacteria for laboratory experiments were isolated from plate cultures of filtered, freshly collected or stored Toussaint lake water. No attempt was made to identify the bacteria although it was observed that all species were Gram-negative rods; the different types were separated on the basis of colonial characteristics alone. Alchem 299, an agar medium produced by Alchem Ltd., Burlington, Ontario for culturing freshwater bacteria, was used for isolation and measurements of growth. Standard bacteriological techniques were used for dilution of bacteria in preparation for measurement of populations. One-tenth-milliliter samples from the dilution tubes were spread evenly over the surface of agar plates with a glass spreader. Three to six plates were prepared for each dilution. Plates were incubated at room temperature for 24-72 hours.

Bacteria for the inoculum were grown in nutrient broth or sterile lake water. When nutrient broth was used, bacteria were centrifuged, washed with distilled water, recentrifuged and resuspended in distilled water. When lake water was used, bacteria were introduced directly into experimental vessels. Experiments were carried out in continuously agitated, Pyrex Erlenmeyer flasks stoppered with cotton wool. Results from contaminated flasks were discarded.

In the first experiments the amount of P^{32} in bacteria was measured by difference. Bacteria were separated from the water by centrifuging five milliliters of the culture at 11,000 r.p.m. for 15 min. Then the radioactivity of two milliliters of the supernatant was measured. In later experiments the amount of P^{32} in bacteria was measured directly. Complete separation of bacteria was accomplished by filtering the culture through Millipore bacterial filters purchased from the Lovell Chemical Company, Watertown, Mass. The filters, which were of a slightly smaller diameter than the counting trays, were dried and tested for radioactivity.

LAKE EXPERIMENT

Description of Lake

Toussaint Lake is a bog lake situated on the property of Atomic Energy of Canada Limited near Chalk River, Ontario. The surrounding terrain is Precambrian granite overlain with a thin layer of postglacial sand. The lake drains an area of approximately 200 hectares, has a surface area of 4.7 hectares and a maximum depth of 9.8 meters. It has a small permanent outlet and two temporary inlets. The water is deep brown. At each end there is a large area of rooted aquatic plants representing the following genera: *Brasenia, Chamaedaphne, Myrica, Myriophyllum, Nuphar, Nymphoides, Potamogeton, Sphagnum* and *Utricularia.*

During the summer there is a stable thermal stratification and by late July the hypolimnion becomes almost devoid of dissolved oxygen (Fig. 2). The summer stratification of inorganic and organic phosphorus (Fig. 2) is similar to that reported by

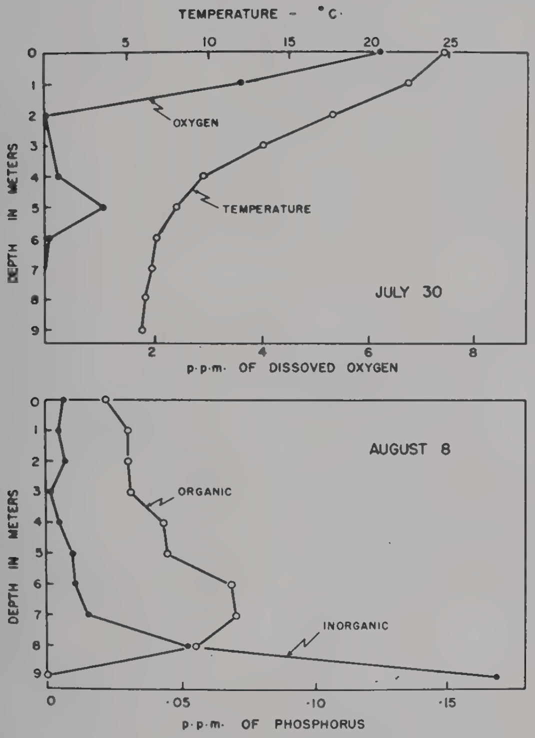

FIG. 2. Typical series of measurements showing variation in temperature, dissolved oxygen, soluble inorganic phosphate and organic phosphorus with depth in Toussaint Lake during tracer experiment.

Hutchinson (1941) in Linsley Pond. From the surface to a depth of seven meters the organic phosphorus concentration was, on the average, eight times as high as the inorganic phosphate, but below seven meters the concentration of organic phosphorus decreased and inorganic phosphate increased sharply with depth. These were the conditions found in the lake when P^{32} was added on July 25, 1951.

Loss of P^{32} from Suspension

To calculate the total P^{32} in suspension or solution the earlier workers assumed that horizontal mixing of P^{32} was complete at all depths. To determine whether this were true in Toussaint Lake, samples for measurement of radioactivity were collected at two widely separated stations. Total suspended P^{32} in the top five meters was calculated from the concentration of P^{32} at each station by the method proposed by Coffin *et al.* (1949) and is shown in Figure 3. Since there was no appreciable difference between the total radioactivity calculated from the concentrations of P^{32} at the two stations, it was concluded that this method was applicable to Toussaint Lake and therefore the total suspended P^{32} was calculated from radioactivity at the central station. "Suspended P^{32}" is used to mean all P^{32} in the open water, both in solution and in plankton. Results are given in Table I. There was a rapid loss of P^{32} from suspension during the first seven days followed by a slower loss during the next 21 days; at the end of four weeks only 23% of the P^{32} remained in suspension.

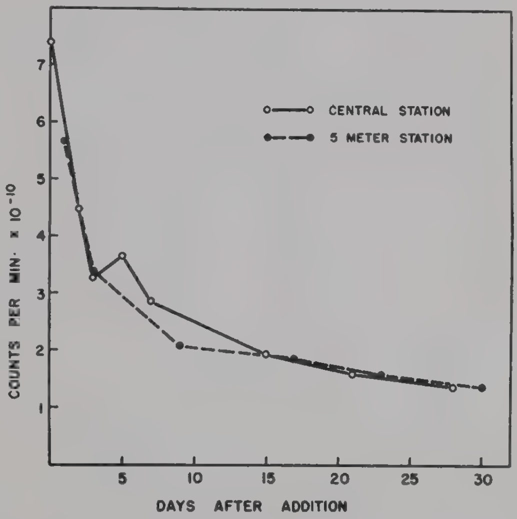

FIG. 3. Total radioactivity in the upper five meters calculated from radioactivity of vertical series of water samples taken at the central station and at the five-meter station.

TABLE I. Amount of P^{32} remaining in suspension in Toussaint Lake after addition of 200 mc. (7×10^{10} c.p.m.) on July 25, 1951

Days after Addition	c.p.m. x 10^{-10}	% of Total
0	7.40	105
2	4.51	64
5	3.74	53
7	2.92	42
15	2.03	29
21	1.96	28
28	1.59	23

Mechanism of Loss from Suspension

There are several ways in which tracer phosphorus could have been removed from the open water; it could have been lost through the outlet, carried down into the bottom mud with sedimenting seston, or utilized by organisms inhabiting the littoral region. Loss through the outlet was calculated (with an error possibly as great as 50%) from volume of flow and radioactivity of outlet water. A total of 1.2% of the added P^{32} was lost through the outlet during the first week and only 0.5% during the last three weeks. Obviously this was not a major factor in the removal of P^{32} from suspension. Loss to bottom sediments was calculated from the radioactivity of 21 mud samples which were taken as described above at depths of 2 to 9.5 meters in a straight line across the lake from east to west. The average radioactivity of mud was $(50 \pm 20) \times 10^3$ c.p.m. per m^2 on August 6, $(30 \pm 3) \times 10^3$ c.p.m. on August 23 and $(45 \pm 4) \times 10^3$ on September 5. No trend is shown by these figures, but if the one extremely high reading from the August 6th series is deleted, the average for that date becomes $(30 \pm 5) \times 10^3$ c.p.m. There is then an indication of a slight increase of radioactivity with time. Nevertheless, the radioactivity of all samples was averaged to give $(42 \pm 8) \times 10^3$ c.p.m. per m^2 and used as an approximation of maximum radioactivity of mud below the two-meter contour. The total surface area of mud below the two-meter contour was estimated to be 5.15×10^4 m^2 (110% of surface area of the lake). From these figures the amount of P^{32} lost to the mud below the two-meter contour was calculated to be 2.2×10^9 c.p.m. or 3% of the total P^{32} added to the lake. Since a total of less than five per cent of the radiophosphorus was lost through the outlet and to the bottom sediments in four weeks it appears that transfer of phosphorus to the littoral region was largely responsible for the rapid decrease of suspended P^{32}.

A better understanding of the fate of P^{32} which was lost from the open water of Toussaint Lake can be obtained by considering the P^{32} content of the epilimnion and of the deeper water separately. For the purpose of this calculation, a depth of two meters will be taken as the lower limit of the epilimnion. Actually, measurements of temperature and dissolved oxygen (Fig. 2) showed that the thermocline extended to the surface at times, and measurements of vertical distribution of P^{32} indicated that it mixed rapidly only to a depth of one meter, but the choice of two meters ensured that all rooted aquatic plants and associated organisms would be included within the "epilimnion."

The changes, during the experiment, of total suspended P^{32} above two meters and of P^{32} both in suspension and in the mud below two meters are shown in Figure 4. P^{32} was rapidly lost from the upper two meters but little passed into the water and mud below two meters or through the outlet. At the end of four weeks 88% of the total P^{32} had been lost from the epilimnion but only 14% had passed below the two-meter level or been lost through the outlet. The remaining 74% had been lost elsewhere, probably to the littoral organisms in the upper two meters.

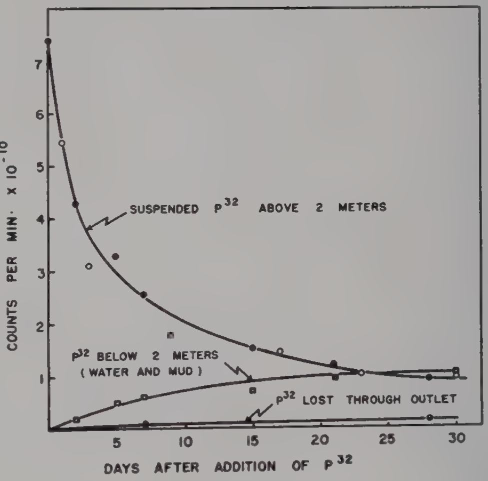

FIG. 4. Loss of P^{32} from the upper two meters of Toussaint Lake (open circles calculated from radioactivity at the five-meter station and closed circles from radioactivity at the central station) and increase in water and mud below two meters. Cumulative loss of P^{32} through the outlet is also shown.

The loss of P^{32} from the epilimnion of Toussaint Lake by no means indicates that there was a depletion of phosphorus during the experiment. Table II shows that there was actually an increase of inorganic phosphate and that organic phosphorus remained relatively constant. Therefore, as well as a loss of phosphorus to the littoral region, there must have been a return of phosphorus from the littoral region to the epilimnion. This situation can be best described as a turnover of the "mobile" phosphorus of the epilimnion with respect to the following exchange:

Mobile P of water and plankton in
epilimnion ⇌ P of littoral solids in
contact with epilimnion

The phosphorus participating in this exchange is described as mobile because it is not known which fraction of the total phosphorus is involved. Probably the inorganic and part of the plankton phosphorus are involved but the soluble organic phosphorus may also enter into the exchange to a limited extent.

When tracer ions or molecules have been added to one phase of a system such as the one described above, the rate of disappearance of tracer can be used to give a measure of the turnover time of the naturally occurring ions or molecules in that phase (Zilversmit *et al.* 1943). The application of this calculation to a system similar to the one described

TABLE II. Weight of phosphorus in the upper two meters of Toussaint Lake during tracer experiment, 1951

Date	Kilograms of Phosphorus	
	Inorganic	Organic
July 23	.072	2.09
Aug. 1	.220	3.08
Aug. 8	.485	2.09
Aug. 15	.628	2.77
Aug. 22	.789	2.76

above has been adequately discussed by Hayes *et al.* (1952) and will not be treated here. From the rate of disappearance of P^{32} from the epilimnion of Toussaint Lake the turnover time of mobile phosphorus was calculated to be 3.6 days. The similarity between this value and the values of 5.4 and 7.6 days obtained by Hayes *et al.* is fortuitous since they calculated the turnover time of inorganic phosphate of the whole lake from the rate of disappearance of P^{32} from filtered water, and did not imply that all or even a large fraction of the P^{32} lost from solution was lost from the open water.

Uptake of P^{32} by Plankton

The percentage of the total suspended P^{32} in the 0-2m and 8-9 m strata which was in the plankton removed by a Foerst centrifuge is shown in Figure 5. At the surface (0-2 m) the percentage of P^{32} in plakton increased rapidly to a maximum of approximately 50% in three days, and remained relatively constant until the end of the experiment although the total amount of P^{32} in this layer decreased continuously. Since P^{32} was lost from the open water to the littoral region, there must have been a rapid equilibration between planktonic phosphorus and inorganic phosphate so that the ratio of P^{32} in solution to that in plankton remained constant.

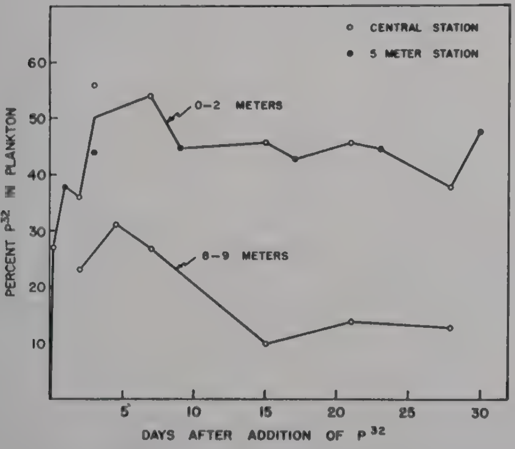

FIG. 5. Percentage of suspended P^{32} of the surface and deep water of Toussaint Lake in the fraction of the plankton removed by Foerst centrifugation.

In the deepest water studied (8-9 m layer) the percentage of P^{32} in solids was consistently lower than at the surface. Since the P^{32} almost certainly reached this depth with sedimenting plankton, it is apparent that there was a rapid regeneration of inorganic phosphate in the hypolimnion. The regeneration may have been more complete than is indicated by these results since there was probably some precipitation of ferric phosphate in the centrifuge.

UPTAKE OF PHOSPHATE BY BACTERIA IN THE ABSENCE OF OTHER PLANKTON

Although it was demonstrated that phosphate is rapidly taken up by plankton in the epilimnion of Toussaint Lake and that there is an exchange of phosphorus between the open water and the littoral region, it is not possible to calculate the actual quantities of phosphorus involved because the specific activities of the various phosphorus fractions are not known. Therefore, it appeared that the value of further lake experiments would be limited until more was known about certain transformations of phosphorus such as the uptake and loss of inorganic phosphate by plankton.

Bacteria and algae are the two groups of planktonic organisms known to take up phosphate from solution in significant amounts. Bacteria were chosen for further study because they were known to take up phosphate rapidly in stored lake water, although their position in the phosphorus economy of lakes was uncertain.

The uptake of phosphate by aquatic bacteria has received relatively little attention because their rapid multiplication has been thought to be peculiar to stored water. Consequently, interest has centered on the cause of bacterial multiplication in such water. Zobell (1943) suggested that growth in stored water occurred on the walls and was stimulated by adsorption and concentration of organic matter on walls of storage vessels. However, Taylor and Collins (1949) were not able to confirm Zobell's hypothesis and proposed that the walls simply acted as a convenient site for attachment and multiplication of bacteria. In spite of their difference of opinion, these workers agreed that increase of bacterial population was due to multiplication of attached bacteria. This is not necessarily the only explanation for the increase of bacterial numbers in stored water, for an earlier suggestion by Waksman and Carey (1935) might be equally valid. They suggested that the bacterial populations of natural waters are held in check by organisms which feed on bacteria and that these predators die off when the water is stored. If this is true, it is possible that there is a rapid turnover of the bacterial populations of natural waters and that bacteria take up considerable amounts of inorganic phosphate in some lakes.

The growth of bacteria in stored lake water was therefore studied to determine if attachment to the walls of storage vessels was essential for multiplication of the species responsible for the uptake of inorganic phosphate.

Preliminary experiments showed that when water from a number of lakes was enriched with inorganic phosphate and stored, there was an initial decrease in the concentration of inorganic phosphate during the first 48 hours, followed by a slow regeneration. This was in accord with previous observations of Waksman and Stokes (1937) and Renn (1937) who also observed an increase in bacterial population coincident with the loss of inorganic phosphate and inferred that the phosphate was utilized by growing bacteria. If, as suggested by Zobell, and Taylor and Collins, some or all bacterial multiplication takes place on the walls of storage vessels, it would be expected that some of the phosphate lost from solution would go to the walls.

Experiment 1

The first experiment was carried out to determine whether phosphate lost from solution remained in suspension or was lost to the walls. Fifteen liters of water was collected from the surface of Toussaint Lake on July 18, 1952 and filtered through a Whatman No. 12 filter paper to remove larger plankton. On the following day the phosphate concentration was increased to .011 p.p.m. by addition of potassium dihydrogen phosphate and P^{32} was added to give approximately 250 c.p.m. per ml. The water was maintained at 15°C and stirred continuously. Samples were taken for measurement of inorganic phosphate, total suspended P^{32} and P^{32} in solution.

Results are shown in Figure 6. Inorganic phosphate and P^{32} in solution decreased rapidly during the first ten hours and then more slowly until, at the end of 32 hours, more than 85% had been lost from solution. Since the loss of P^{32} from solution paralleled that of inorganic phosphate, it appears that there was a direct removal of phosphate from solution and not a turnover of phosphate.

At no time during the experiment was there a significant loss of P^{32} from suspension. Therefore, it is obvious that phosphate was removed from solution by living or non-living, suspended, particulate matter of a size which would pass through filter paper and was not lost to the walls of the storage vessels.

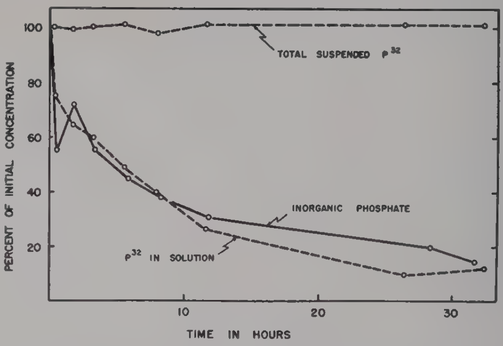

Fig. 6. Loss of P^{32} and inorganic phosphate from solution and total suspended P^{32} in filtered, Toussaint Lake water stored in a Pyrex container. Initial concentration of inorganic phosphate was .011 p.p.m.

Experiment 2

To demonstrate that bacteria could cause the loss of inorganic phosphate from solution observed in the previous experiment, the uptake of phosphate by pure cultures of aquatic bacteria was measured. Uptake of P^{32} was used as a measure of uptake of inorganic phosphate and, as in the previous experiment, loss of P^{32} from suspension as a measure of attachment of bacteria to the walls. Of six species isolated and tested, five grew in autoclaved lake water and utilized inorganic phosphate during their growth phase. The species used differed in the extent to which they attached to the walls during growth: the two extreme results are shown in Figure 7. In culture 1 the P^{32} taken up was equally distributed between bacteria in suspension and bacteria attached to the walls during the growth phase. A decrease in the percentage of P^{32} on the walls and an increase in suspended P^{32} after 20 hours' incubation suggested that as the culture aged, the cells broke away from

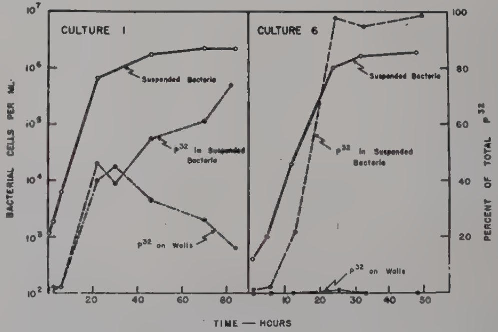

Fig. 7. Uptake of P^{32} by suspended and sessile cells of two species of bacteria during growth in stored Toussaint Lake water.

the walls and remained in suspension. In culture 6 there was no significant loss of P^{32} to the walls during or on completion of bacterial growth. It appears that all the cells of this species remained in suspension during and on completion of growth.

In control flasks containing sterile lake water there was almost no loss of P^{32} from solution. The average loss from controls of all experiments was 1.8%.

Conclusions

Since there was almost no loss of P^{32} from solution when sterile lake water was stored in Pyrex vessels, adsorption of phosphate on walls or suspended inanimate material was of no importance in causing the decrease of inorganic phosphate. Pure cultures of aquatic bacteria are capable of causing this decrease, presumably by utilizing inorganic phosphate for their growth. The multiplication of some species which utilize inorganic phosphate may take place on the walls of storage vessels but other species grow well in suspension. The species which multiply in unsterilized Toussaint Lake water do not need to adhere to the walls in order to grow. Therefore, it appeared that the rapid multiplication of aquatic bacteria might not be peculiar to stored water. If this is true the problem has an important bearing on the circulation of phosphate in lakes because studies by Birge and Juday (1934), Kusnetzow and Karzinkin (1931) and Bere (1933) have shown that the bacterial population of lake water is of the order of 10^4 to 10^6 cells per ml. The multiplication of populations of this magnitude must be an important factor in the removal of phosphate from solution.

Uptake of Phosphate by Bacteria in the Presence of Other Plankton

In the preceding laboratory experiments the uptake of phosphate by bacteria was studied in the absence of other plankton: in the following experiments, it was studied in water in which all of the naturally occurring plankton was present. Radioactive phosphorus was added to unfiltered, unsterilized water which was later filtered to fractionate the plankton.

In order to study uptake of P^{32} under completely natural conditions, tracer would have to be added to the whole lake but this is not practicable. Since the results of the first experiment in Toussaint Lake indicated that uptake of P^{32} by plankton might not be complete for several days (Fig. 5) it did not seem advisable to carry out experiments in glass containers in the laboratory where effects of storage would be pronounced. Therefore, in order to make experimental conditions approach natural conditions as closely as possible, the first experiment was carried out in a large polyethylene bag which was suspended in the lake. This experiment showed that uptake of P^{32} was complete in the time required to bring to the laboratory and filter the first samples. Consequently, the remaining experiments were carried out in the laboratory, but owing to the short period of time involved in these experiments, it was considered that the results would be comparable with those obtained from water under natural conditions.

Polyethylene Bag Experiment

Methods. The first experiment was carried out on August 28, 1953 in a cylindrical polyethylene bag two meters in diameter and one and one-half meters deep. The bag was suspended at the surface by a circular polyethylene float attached to the rim and fastened to a wooden frame anchored near the center of Toussaint Lake. After the bag had been filled with surface water, 0.4 mc. of P^{32} was added and mixed thoroughly with an oar. One-liter samples of water were taken at different depths within the bag at one, three and five hours after addition of P^{32} and immediately taken to the laboratory where the whole sample was filtered through No. 10 silk bolting cloth to remove large zooplankton. Then 50 ml was filtered through No. 20 silk bolting cloth to remove smaller zooplankton and larger phytoplankton, through No. 2 Whatman filter paper to remove smaller phytoplankton and finally through a Millipore filter to remove bacteria. All filters which were used had been cut to fit the standard counting trays so that they could be dried and counted directly. A 10-ml sample of the filtrate was evaporated and counted.

Results. Since the results from samples taken at different depths were essentially the same, they were averaged for presentation in Table III. The uptake of P^{32} was much more rapid and complete than was expected on the basis of the lake experiment. When the first samples were filtered, one and one-half hours after the P^{32} was added, over 97% of the P^{32} had been taken up by plankton. After this time the percentage of P^{32} in the plank-

Table III. Per cent of total P^{32} in fractions of plankton and in solution at intervals after addition of tracer phosphate to water inside a polyethylene bag August 28, 1953

Fraction	1.5 hr.	4.5 hr.	6 hr.
No. 10 Bolting cloth	0.9	1.3	3.4
No. 20 Bolting cloth	1.9	1.8	1.5
No. 2 Whatman Paper	33.8	28.9	21.3
Millipore Filter	60.4	63.2	68.4
Filtrate	2.9	4.8	5.2

ton decreased slightly. At the end of six hours when 95% of the P^{32} was in the plankton only five per cent of the total P^{32} had been taken up by zooplankton and larger phytoplankton; by far the largest amount (68.4%) had been taken up by the fraction of the plankton which passed through filter paper and was removed on the Millipore filter.

The concentration of inorganic phosphate within the bag changed only slightly during the experiment: it was .0020 p.p.m. at the beginning and .0018 p.p.m. at the end. But P^{32}, and hence phosphate, was taken up by plankton. Therefore, phosphate must have been returned to the water at the same rate as it was removed. These results are best explained by postulating a turnover of inorganic phosphate caused by the simultaneous uptake and release of phosphate by plankton. Since the uptake of P^{32} was complete when the first samples were analysed this experiment gave no measure of the rate of turnover.

Laboratory Experiments

In the following experiments the turnover of inorganic phosphate and the uptake of P^{32} by plankton was studied in water which had been brought into the laboratory. Since all experiments were of short duration, it was assumed that water and plankton would not be changed appreciably by storage in small containers.

Methods. Surface water was collected from the center of Toussaint Lake, immediately transferred to the laboratory and poured into experimental vessels. A ten-liter sample was used in the first experiment and a one-liter sample in the second. Radioactive phosphorus was added to give 100-200 c.p.m. per ml and the first samples were taken for filtration as soon as possible. Filtration took 10-30 sec.; the mid-time of filtration was recorded. Water was stirred after the addition of P^{32} and before each sampling. During these experiments the water was illuminated by skylight and by a 15-W daylight fluorescent lamp.

To determine whether algae, as well as bacteria, passed through the filter paper, the filtrate was examined microscopically. Surface water for this purpose was collected from Toussaint Lake on September 10, 1953 and October 27, 1953 and again on September 28, 1954 when a third measurement of turnover rate of inorganic phosphate was also made. The plankton in unfiltered water, in water filtered through No. 20 bolting cloth and No. 2 Whatman filter paper was concentrated by means of Sedgwick-Rafter funnels on September 10, 1953, a Foerst centrifuge on October 27, 1953 and an International No. 1 centrifuge running at 3,000 r.p.m. on September 28, 1954. All algae and algal fragments in the concentrates were counted.

Results. Loss of P^{32} from solution and uptake by the two plankton fractions is shown in Figure 8. Since all experiments to measure turnover gave essentially the same results, only the series made on Sept. 18, 1953 is presented. There was a rapid loss of P^{32} from solution—in 20 minutes when equilibrium had been attained, approximately 93% of the added P^{32} had been taken up by plankton. Again the fraction retained by the Millipore filter took up more than half of the added P^{32}. Phosphate concentration was approximately .0008 p.p.m. and did not change during the experiment. Therefore, the uptake of P^{32} represents a turnover, not a direct uptake, of phosphate. Turnovertime was calculated from the semi-log plot of loss of P^{32} from solution and was found to be 3.6 min. on September 11, 1953 and 5.4 min. on September 18, 1953. This is more rapid than was expected on the basis of the work of Hayes *et al.* (1952) and Whittaker (1953) and from results of the 1951 experiment in Toussaint Lake. It is believed that earlier work did not give a true measure of the rate of turnover of phosphate because the methods of separating plankton did not completely remove the smallest plankton which were shown above to be most important in causing turnover of inorganic phosphate.

Results of the algal counts are given in Table IV. The bolting cloth removed an average of 66% of the algal cells. The largest algae such as *Dinobryon* and *Asterionella* were almost completely removed by this filter. An average of 98% of the total algal cells were removed by the filter

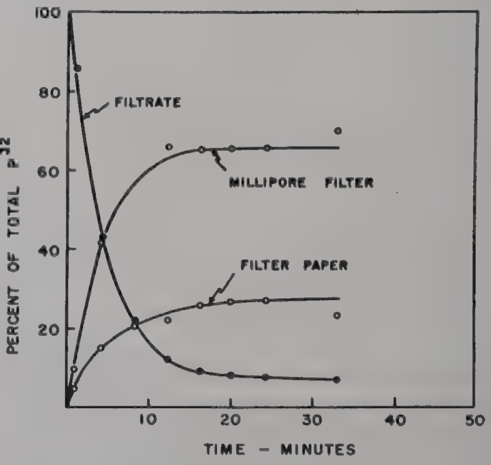

FIG. 8. Loss of P^{32} from solution in Toussaint Lake water and uptake of P^{32} by the plankton removed on a Whatman #2 filter paper and by the fraction of the plankton which passed through the filter paper and was removed on a Millipore filter, Sept. 18, 1953.

paper. Therefore, since a very small percentage of the algal plankton passed through the filter paper to the Millipore filter and since on each of the three dates the bolting cloth and filter paper fractions took up much less P^{32} than the Millipore filter fraction, it was concluded that bacteria were the organisms which caused the turnover of inorganic phosphate. Also, it is possible, although it was not demonstrated, that a large part of the radioactivity of the filter paper fraction was caused by bacteria which were retained by the filter paper.

TABLE IV. Total number of algal cells in unfiltered and filtered Toussaint Lake water, as determined by microscopic counts

	ALGAL CELLS PER ML			
	Sept. 10 1953	Oct. 27 1953	Sept. 28 1954	Average per cent removed
Unfiltered water......	900	3200	860	—
Filtrate of No. 20 bolting cloth.......	230	1400	—	66
Filtrate of No. 2 Whatman paper....	13	17	35	98

Disappearance of Added Phosphate

It was shown in the previous experiments that, although there was a rapid turnover of inorganic phosphate in Toussaint Lake water, the concentration of phosphate remained constant for as long as six hours. Obviously the rate of uptake of phosphate was exactly balanced by the rate of loss in these experiments. In order to determine the effect on this equilibrium of changing the concentration of phosphate in the water, the concentration was measured at intervals after addition of small quantities of inorganic phosphate to Toussaint Lake water.

Surface water was collected from the center of Toussaint Lake and divided into three two-liter samples. The phosphate concentration of the first sample was unaltered, the second was increased by .001 p.p.m. and the third by .005 p.p.m. The samples were placed in a water bath and maintained at the same temperature as when collected. Phosphate analyses were carried out as often as possible over a six hour period.

The experiment was repeated three times and the results of all tests were essentially the same. The results of the most complete series are shown in Figure 9. As was expected, the phosphate concentration in the unaltered sample remained almost constant, but in the samples to which phosphate had been added it decreased rapidly until it reached approximately the original concentration. It appears that under natural conditions the concentration of inorganic phosphate is maintained at a level where the rate of uptake by plankton is balanced by the rate of loss from plankton and that no increase of plankton phosphorous is possible unless the water receives an increment of phosphate from the inflowing water or from the littoral region. When the inorganic phosphate is added to the water the rate of loss by plankton remains constant but the rate of uptake increases until the concentration of phosphate in solution drops back to its original value and equilibrium between uptake and loss by plankton is re-established.

The initial increased rate of uptake, averaged from all tests was between 2×10^{-5} and 3×10^{-5} µg/ml/min. This increased rate of uptake is quite small in comparison with the turnover rate which was 17×10^{-5} µg/ml/min. It might be expected that the rate of uptake should be higher when .005 p.p.m. of phosphate was added than when .001 p.p.m. was added. If this is true the difference was small and was not detected in the limited number of tests carried out.

Comparison between Turnover of Phosphate in Toussaint Lake and in Other Lakes

Although it was shown that the turnover time of phosphate in Toussaint Lake was extremely short and that planktonic bacteria were largely responsible for causing this turnover, it is possible that Toussaint Lake might be exceptional in these respects. Therefore, the turnover of phosphate was measured in several other lakes for comparison with Toussaint. Water was tested from Oiseau Lake, a small, colorless, oligotrophic lake; Maskinonge Lake, a large, slightly coloured oligotrophic lake, and from the Ottawa River which, in the vicinity of Chalk River, more closely resembles a large lake than a river.

The results are summarized in Table V. It can be seen from column 3 that the turnover time of phosphate in Toussaint Lake was not exceptionally short since Oiseau and Maskinonge Lakes had turnover times for inorganic phosphate of 3.6 and 26 minutes respectively. However, the turnover time in Ottawa River water (30 hours) was very much longer than in any of the lakes. Since turnover time is a function of phosphate concentration as well as of plankton metabolism, it is perhaps preferable to compare the rate of turnover of phosphate in the different waters. In this respect, also, the three lakes were similar, while the turnover rate in Ottawa River water was much slower (Table V). Although it is not wise to make generalizations from so few results it does appear that the rapid turnover of inorganic phosphate is not peculiar to Toussaint Lake but is common to lakes

TABLE V. Comparison of phosphate turnover in several lakes in the vicinity of Chalk River, Ontario

Lake	Area in hectares (1)	PO_4 conc. p.p.m. (2)	Turnover time (3)	Turnover rate (µg/ml/ min.) (4)	Ratio of max. P^{32} in M.F. fraction to P^{32} in F.P. fraction (5)
Oiseau 28/IX/54......	3.6	.0003	3.6 min.	0.8×10^{-4}	3.8
Toussaint 11/IX/53 & 18/IX/53*.....	4.7	.0008	4.5 min.	1.8×10^{-4}	2.5
Maskinonge 17/IX/54......	160	.0012	26 min.	0.5×10^{-4}	1.8
Ottawa River 14/IX/54......	—	.0049	30 hr.	0.03×10^{-4}	2.2

*Average for the two dates is tabulated.

in this region, whether oligotrophic or acid-bog, that have a low concentration of inorganic phosphate.

To give an indication of the importance of the Millipore filter fraction of the plankton in causing turnover of inorganic phosphate in the different lakes, the ratio of the maximum radioactivity in the Millipore filter fraction to the maximum radioactivity in all larger plankton was measured and is given in Table V. It is apparent that in each of the waters tested, the Millipore filter fraction took up appreciably more P^{32} than the larger plankton organisms.

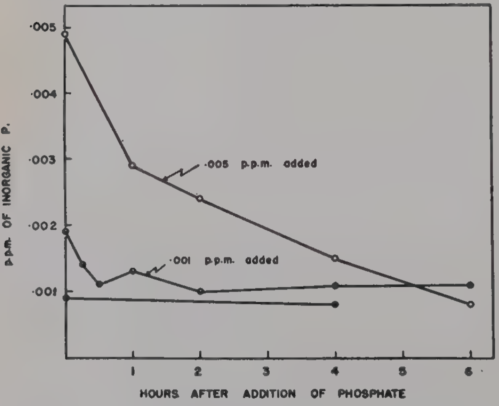

FIG. 9. Concentration of inorganic phosphate in water from the surface of Toussaint Lake measured at intervals after the addition of (i) .005 p.p.m. of inorganic phosphate, (ii) .001 p.p.m. of inorganic phosphate and (iii) no phosphate.

DISCUSSION

The results presented in this paper emphasize more strongly the transient nature of inorganic phosphate in the epilimnion of small lakes, already demonstrated by the earlier tracer studies of Hutchinson and Bowen 1950), Coffin *et al.* (1949) and Hayes *et al.* (1952). It is shown that inorganic phospate remains constant at a low concentration for periods as long as several hours, not because plankton are unable to take up phosphate, but because the rate of uptake does not exceed the rate of metabolic loss, and that the inorganic phosphate in solution in the water is replaced many times in an hour.

The turnover times of inorganic phosphate in the small lakes studied were quite different from the estimates of turnover times (5-8 days) in two Nova Scotia lakes presented by Hayes *et al.* (1952). No doubt the extreme rapidity of turnover observed in lakes in the Chalk River district was related to the low concentrations of inorganic phosphate in these waters: in lakes with higher concentrations the turnover time might be expected to be much longer. Nevertheless it is believed that Hayes' values may be high because his methods of separating plankton from the water did not remove all bacteria which have been shown in the recent investigation to be most active in causing turnover of inorganic phosphate. In future studies of phosphate metabolism in lake water or of uptake of phosphate by plankton, the activity of aquatic bacteria must be considered and care should be taken to distinguish between uptake by algal plankton and uptake by bacteria.

The uptake of phosphate by bacteria in lake water certainly requires more study because planktonic bacteria, if they take up small increments of phosphorus received from inflowing water or from marginal vegetation, may compete with algae for this essential element. Whether this would be advantageous in terms of productivity is an interesting point. Bacteria are not generally autotrophic; they primarily transform existing organic matter, either particulate or dissolved, into bacterial protoplasm, a form that can be utilized by zooplankton. If, in this process, they utilize inorganic phosphate, they would reduce the amount of phosphate available to algae and thus reduce the amount of organic matter produced by algae. Since our present knowledge of the utilization of either bacteria or algae by zooplankton is incomplete, it is not possible to say what effect the utilization of phosphate by bacteria would have on productivity.

In addition to the rapid exchange of inorganic phosphate between water and plankton, a slower exchange of phosphorus between the open water of the epilimnion and littoral organisms was demonstrated. In Toussaint Lake the turnover time of "mobile" phosphorus in the epilimnion during the last week of July was found to be 3.5 days. In larger lakes and in lakes with fewer littoral organisms the turnover of phosphorus between open water and the margin would be much slower and of little or no importance in determining the amount of phosphorus in the epilimnion, but in Toussaint Lake a slightly greater uptake or loss by the littoral organisms could greatly decrease or increase the total phosphorus of the epilimnion within a few days.

A rapid turnover of phosphorus of the epilimnion has also been demonstrated in Linsley Pond by Hutchinson and Bowen (1950). But it differed from the turnover in Toussaint Lake in that phosphorus, although it entered the epilimnion from the littoral region, was lost almost exclusively to the hypolimnion. In Toussaint Lake there was also a loss to the hypolimnion but it was insignificant in comparison with loss to the littoral region.

Finally, little is known about the position of soluble organic phosphorus compounds in the phosphorus cycle of natural waters. This is a serious gap in our knowledge since organic phosphorus is usually present in much higher concentration than inorganic phosphorus. It is generally assumed that organic phosphorus compounds are produced by decomposition of plant and animal tissue, but nothing is known about the rate of production or the possible utilization of these compounds. Until the position of organic phosphorus in the phosphorus cycle is established, conclusions based on tracer studies with inorganic phosphate will tell an incomplete story and may even be misleading. For example, in the calculation of turnover time of inorganic phosphate, it has been assumed that all P^{32} in solution was in the form of inorganic phosphate. But if some of the soluble organic phosphorus compounds in water are produced by plankton, P^{32} would soon be incorporated into these compounds. Calculations of the specific activity of inorganic phosphate based on the amount of P^{32} in solution would then be erroneous. Therefore, a study of organic phosphorus compounds in the lake water is essential for complete interpretation of tracer experiments. It is to be hoped that with more widespread application of the tracer technique in limnological research the position of soluble organic phosphorus in the phosphorus metabolism of lakes will be clarified.

SUMMARY

The phosphorus cycle in a small, acid-bog lake was studied by the use of radioactive phosphorus. Of the total P^{32} added to the surface, 77% was lost from the water and plankton in four weeks but only two per cent was lost through the outlet and three per cent to the mud. It was concluded that there was a turnover of "mobile" phosphorus of the epilimnion with phosphorus of the littoral organisms. The turnover time of phosphorus of the epilimnion with respect to this exchange was found to be 3.5 days. The similarity between this value and the turnover times of inorganic phosphate calculated by Hayes *et al.* (1952) is considered to be fortuitous.

Several days after the addition of P^{32} to the lake, 50% had passed into the fraction of plankton removed by a Foerst centrifuge. This was similar to the results of Hutchinson and Bowen (1950) and Whittaker (1953) who used comparable methods for the removal of plankton. Laboratory experiments showed that neither a Foerst centrifuge nor filter paper removed the organisms which took up P^{32} most rapidly. When complete removal of plankton was achieved by filtering water through a Millipore bacterial filter it was shown that over 95% of the added P^{32} was taken up by plankton within 20 minutes. The turnover time of inorganic phosphate in the surface water of Toussaint Lake was approximately five minutes. Measurements of turnover made in two other small lakes suggested that a rapid turnover of inorganic phosphate is not peculiar to Toussaint Lake.

In laboratory experiments with mixed and pure cultures of aquatic bacteria, loss of P^{32} from solution and loss from suspension were used to measure uptake of phosphate by bacteria and extent of attachment of bacteria to the walls of glass containers respectively. Growing bacteria rapidly utilized inorganic phosphate from lake water but when sterile water was stored there was no loss of phosphate from solution. Attachment to the walls was not essential for the growth of most species of bacteria which multiplied and utilized phosphate during the first few days of storage.

The turnover of phosphate under natural conditions appeared to be caused primarily by bacteria. It was concluded that aquatic bacteria might compete with algae for inorganic phosphate.

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THE DAILY ACTIVITY RHYTHM OF *DROSOPHILA SUBOBSCURA* AND *D. OBSCURA*[1]

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Despite the great amount of information available on the genetics of Drosophila, comparatively little is yet known about the ecology of the species which comprise this genus. With the extensive use of these organisms for studies of population genetics and speciation, ecological information becomes all the more important. In this connection, continued analysis of the response of Drosophila to environmental conditions seems worthwhile.

Although some information is available on the diurnal periodicity of Drosophila, very little is known about differences in activity between closely related species. While studying the distribution of Drosophila in England, it became clear that two closely related species, *D. obscura* and *D. subobscura,* could both be caught in large numbers in the same locality, and a comparison of the activity of these two species under the same environmental conditions was thus possible. In order to make these comparisons, collecting was planned at certain localities and measurements were made of temperature, humidity, and light at the time of each round of collecting. The object was two-fold: firstly, to try to describe the conditions of the several environmental factors at which various levels of activity occur; secondly, to see if the activity patterns vary between species.

Methods

The number of flies coming to bait was recorded as a method of determining the diurnal periodicity. The collecting method used was a modification of that described by Spencer (1950). Stringed wax-paper cups, containing fermenting bananas, were hung on small branches or rough bark of trees, at approximately one meter from the ground and at an angle of about 45°. The flies were removed by approaching the cup quietly, placing an inverted funnel over the opening, and transfering the flies into a vial. For an all-day series of collections, the cups were set out in a given habitat in the evening, and collecting rounds made on the following day at intervals of 1½ to 2 hours, from before dawn until after dark. Temperature, humidity, light, and in some cases wind velocity, were recorded at the time of each collection in the same spot (usually the center) in the collecting area.

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[1] The following account has been considerably reduced for publication from the complete data in a D. Phil. thesis "The taxonomy and ecology of the British species of *Drosophila*." One copy of the thesis is deposited in the Bodleian Library, Oxford; another in the library of the Department of Zoology and Comparative Anatomy, Oxford University.

[2] This work was made possible by the hospitality of Professor A. C. Hardy of the Department of Zoology and Comparative Anatomy, Oxford University. I wish to thank Drs. A. J. Cain and P. M. Sheppard of Oxford University for their help and encouragement while supervising this work. Drs. D. J. Finney and M. R. Sampford, now of Aberdeen University, Scotland, aided in the mathematical analysis of the data. The work was supported first by a Fulbright Fellowship and then by a National Science Foundation Predoctoral Fellowship.

Measurements were made as follows: temperature at a height of approximately one meter above the ground with a Centigrade thermometer which was shielded from the sun; humidity at approximately one meter above the ground with a sling psychrometer; light with a Weston Master II Universal Light Meter, measuring the light reflected from a washable white plastic card placed on the ground; wind by an airmeter (lent by the Air Ministry, Harrow, Middlesex). Considerable variation in environmental factors, most notably light, occurred over the collecting area, but only those variations appearing within approximately a meter radius of the observation place were recorded. The flies collected during each round of the traps were stored separately and identified in the laboratory the following day. This ensured positive identification of the closely related species *D. obscura* and *D. subobscura,* which differ morphologically from each other only slightly.

The activity investigated in this study, therefore, is "the flight in search of food which leads the flies to enter traps" (Dobzhansky and Epling 1944). The method of collecting with bait was adopted to facilitate comparison of my results with those of Timoféef-Ressovsky (1940), Dobzhansky and Epling (1944), Pavan *et al.* (1950), Mitchell and Epling (1951) and others. That the variations in number of flies caught throughout the day reflects a difference in Drosophila activity (and not a difference in the attraction radius of the bait, possibly caused by changes in environmental conditions) is indicated by the fact that collections of *D. subobscura* made by suction traps (Taylor and Kalmus 1953) showed a similar pattern of variation in numbers of flies caught throughout the day to that which I found in my collections of the same species, using bait.

MATHEMATICAL ANALYSIS

The data from all-day collections and afternoon collections made during the summer of 1952 and 1953 were analysed mathematically (with advice and aid from the Institute of Design of Experiment, Oxford University) as regressions of activity on temperature, humidity, and light. In these analyses, "activity" is measured as the ratio of the size of a particular catch to the total catch within a certain period of time.

Because of the nature of the interrelationship between light and activity both of *D. subobscura* and *D. obscura* (see Figs. 4 and 10) in the mathematical analysis, light intensities greater than 6.5 candles per sq. ft. are considered separately from light intensities of less than 6.5 candles per sq. ft. The temperature in England rarely rises above 15°c, except during the months of June, July and August; collections made during these three "summer" months are, therefore, considered separately in the analysis of the data. Collections made during the rest of the year are grouped together as "winter" collections. Furthemore, collections made in the meadow are analysed separately from those made in the woodland. Since no effect of wind velocity could be detected on the occasions when it was measured, it will not be discussed any further. "Collection" refers to the number of flies caught during a round of the traps (each round being made approximately every 1½ hours during a collecting period).

The activity patterns discussed in this paper were observed in collecting done over a period of almost three years. However, in this article data are used only of those days for which full records of environmental conditions, as well as variations in numbers of flies caught, were available.

COLLECTING LOCALITIES

Three types of habitat (dense woodland, open woodland, and open meadow) were chosen for this work. The dense woodlands (both in Wytham Woods, Berks) were a deciduous plantation (dominant tree *Acer pseudoplatanus:* D.B.H. approximately 20 cm) and a coniferous plantation (dominant tree *Abies* sp.: D.B.H. approximately 12 cm). In both these woodlands the trees were of more-or-less uniform size, and very little light penetrated the canopy. The open woodland (at Scoulton, Norfolk) was a mixed deciduous-coniferous woodland where the trees were of unequal size and no closed canopy was formed. The open meadow (Wytham Woods, Berks) was an extensive pasture grazed by sheep, adjacent to the deciduous dense woodland described above.

D. SUBOBSCURA: SUMMER

D. subobscura is widely distributed in England, occurring both in dense woodlands and in open meadows, and exhibits a different pattern of activity in these two types of habitat. In dense woodlands (*i.e.* those with a dense leafy canopy) the activity begins at dawn, continues (with some indication of a morning peak) throughout the day, and rises to a marked peak in the evening (see Fig. 1). In the open meadow, there is an abrupt morning and evening peak of activity (the evening peak occurring later than in the woodland) and very few flies are caught during the middle of the day (see Fig. 2). In open woodlands (*i.e.* those where the trees are of unequal height and no dense canopy is formed) *D. subobscura* shows an intermediate pattern of activity, with a marked peak of abundance of flies in the morning and evening, but some activity in the middle of the day (see Fig. 3).

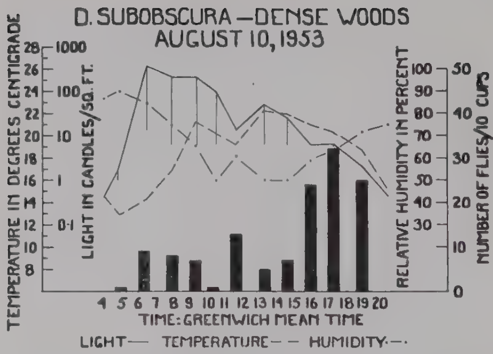

FIG. 1. Collections made in the dense deciduous woodland showing temperature, humidity, light, and the number of *D. subobscura* caught (10 traps set out).

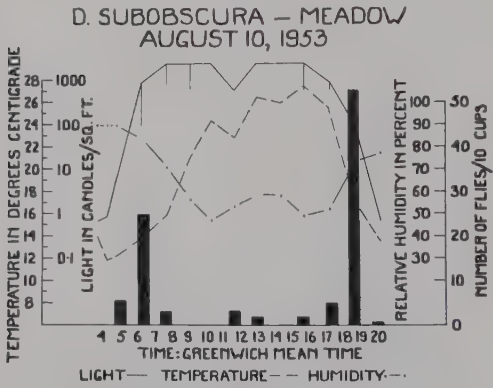

FIG. 2. Collections made in the open meadow showing temperature, humidity, light, and the number of *D. subobscura* caught (20 traps set out).

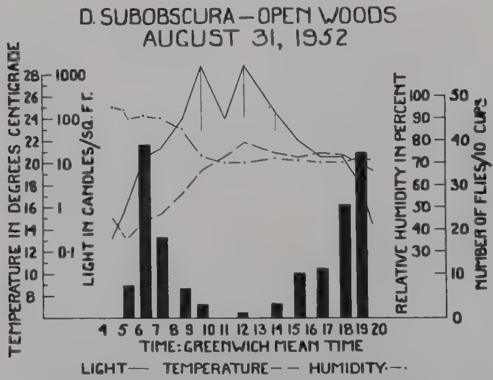

FIG. 3. Collections made in the open woodland showing temperature, humidity, light, and the number of *D. subobscura* caught (10 traps set out).

Summer afternoon collecting of *D. subobscura* in southern England yields a peak in abundance of flies as the light begins to decrease in the evening, followed by a sharp drop in numbers of flies as it gets dark. The mathematical analysis of both afternoon woodland and afternoon meadow collection data shows a highly significant regression ($P < .001$) of activity on light intensities both above and below 6.5 candles per sq. ft. There is no significant regression with either temperature or humidity after the regression on light has been taken into consideration. Thus, variations in light intensity, but not in temperature or humidity, explain the afternoon activity of *D. subobscura* in the woodland. Figure 4 illustrates the relationship between activity and light for woodland afternoon collections; there is an increase in activity with the decrease in light intensity from approximately 100 to 6.5 candles per sq. ft.; when the light intensity drops below 6.5 candles per sq. ft. the activity decreases until it ceases at light intensities below 0.2 candles per sq. ft. The distribution of points indicates a narrow range of optimum light around 6.5 candles per sq. ft., which is substantiated by data from meadow evening collections.

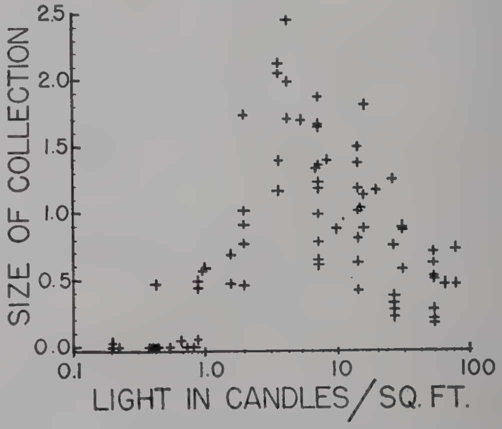

FIG. 4. Afternoon woodland activity of *D. subobscura* in relation to light. (Activity is measured as the ratio of the size of a particular collection to the average size of collection made that day between 2:00 P.M. and 9:10 P.M.)

Morning collections in the dense woodland show no consistent peak of abundance of flies. The mathematical analysis in this case shows a significant regression of activity on both light intensity less than 6.5 candles per sq. ft. ($P < .001$) after temperature has been taken into consideration and on temperature ($P < .01$) after light has been taken into consideration. This would indicate that in the early morning, an increase in the number of flies caught follows both an increase in light intensity and an increase in temperature.

When the light intensity is greater than 6.5 candles per sq. ft., there is no significant regression of activity on light intensity (after the regression on temperature has been taken into consideration), but a significant regression ($P < .05$) of activity on temperature remains (after the regression on light has been taken into consideration). The regression line has a negative slope, and would seem to indicate a sharp decrease in activity with increases in temperature from 15° to 24°C. Since the more extensive data from afternoon collecting show that the largest numbers of flies are caught at approximately 20°C, it seems unlikely that the above relationship is causal. A probable explanation may be that morning changes in temperature are indicating, more accurately than the light meter, increases in light intensity, which in turn lead to a decrease in abundance of flies. This would be consistent with the conclusions reached from the data of afternoon collections.

The effect on morning activity of both temperature and light (when light is less than 6.5 candles per sq. ft.) would provide an explanation as to why the morning maxima (occurring at temperatures of about 14.5°C) are usually smaller and show up at higher light intensities than the evening maxima (occurring at temperatures of about 19.5°C). When the light intensity in the morning is optimum, the temperature is too low; but by the time the temperature becomes optimal, the light is too intense. The effect of the two factors, temperature and light, are more clearly shown during "winter" collections, and confirm the conclusion that at temperatures below 15°C activity is considerably reduced.

D. SUBOBSCURA: WINTER

A quite different pattern of activity is found in early spring or late autumn (Fig. 5), when the activity and temperature curves follow each other very closely. A summary (Fig. 6) of "winter" collections (made during the months of April, May, September, November and December 1952; and January, April and May 1953) indicates that there is very little activity below a temperature of 10°C. Above that temperature, activity begins, but large numbers of flies are not caught at temperatures below 15°C. Although within the range of light intensity of 2 to 20 candles per sq. ft. temperature seems to determine the numbers of flies caught (Fig. 5), large collections are not obtained at light intensities of above 100 candles per sq. ft. or below 1 candle per sq. ft. even if temperature is optimal (Fig. 6).

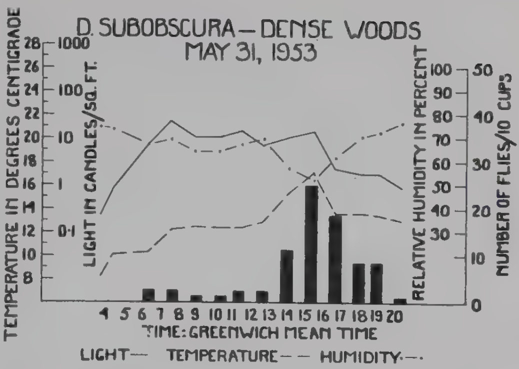

FIG. 5. Collections made in the dense deciduous woodland showing temperature, humidity, light and the number of *D. subobscura* caught (10 traps set out).

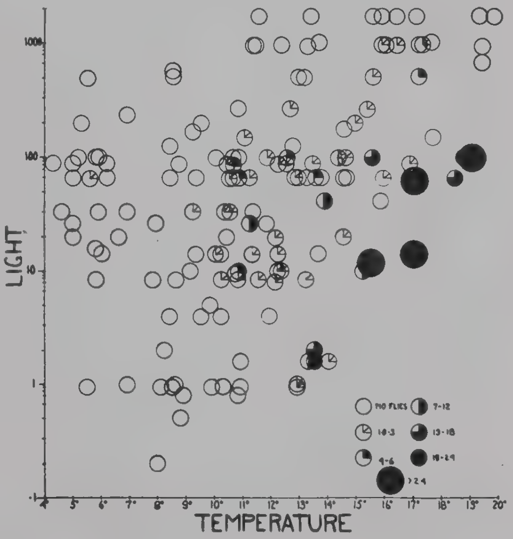

FIG. 6. The activity of *D. subobscura* in relation to temperature and light in collections made during April, May, September, November and December, 1952; and January, April and May 1953. (Temperature and light conditions at the time of each collection are represented by the position of the circles and activity by the black area of the circle.)

D. SUBOBSCURA: CONCLUSIONS

It would appear from the above data that in the summer (when temperatures are above 15°C during most of the day) the pattern of activity of *D. subobscura* is determined by light; and that temperature has a secondary influence (under conditions usually found during an English summer day) which usually leads to a lower maximum in the morning than in the evening. In contrast to summer activity, the activity pattern found in early spring and late autumn (when temperatures are usually below 15°C) appears to be determined primarily by temperature; and light has only a subsidiary effect, leading to an absence of flies when the temperature is above 10°C but the light is very intense, or very low. The difference between "summer" and "winter" patterns of activity results from differences in environmental conditions, not time of year, since on warm days in April and May, a "summer type" pattern of activity was observed.

D. OBSCURA: Summer activity

D. obscura is restricted to woodland habitats, and was caught in large numbers only during the months of June, July and August. Observations do not, therefore, cover as wide a range of environmental conditions as those for *D. subobscura*. No constant pattern of activity was found and striking variations occurred even on different days within the same woodland. The maximum number of flies was caught sometimes in the evening, sometimes in the morning, sometimes in the middle of the day (see Figs. 7-9). The only general pattern which was found was a beginning of activity at dawn, fluctuations in numbers throughout the day, and a cessation of activity after dusk.

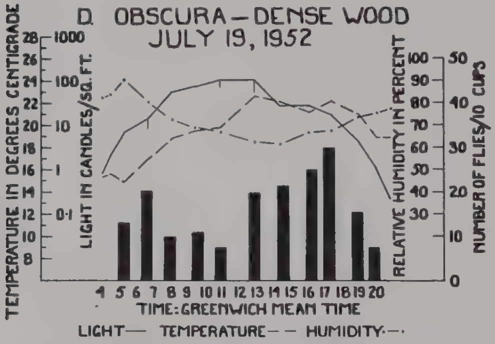

Fig. 7. Collections made in the deciduous dense woodland showing temperature, humidity, light, and the number of *D. obscura* caught (10 traps set out).

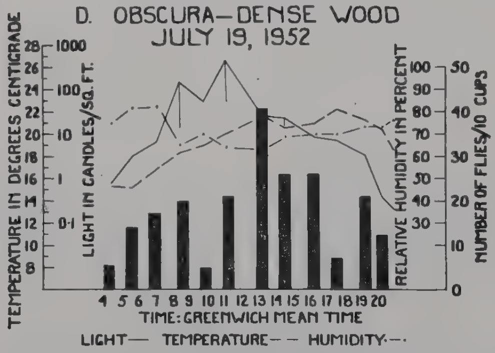

Fig. 8. Collections made in the dense deciduous woodland showing temperature, humidity, light and the number of *D. obscura* caught (10 traps set out).

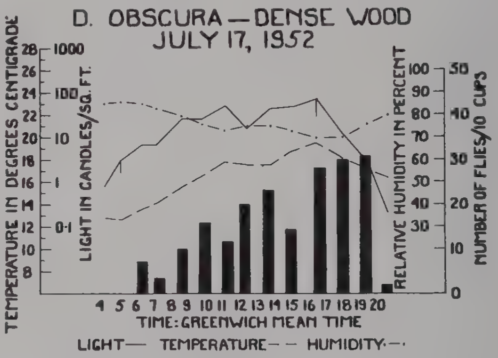

Fig. 9. Collections made in the coniferous dense woodland showing temperature, humidity, light, and the number of *D. obscura* caught (10 traps set out).

In the mathematical analysis of afternoon collections, only the regression of activity with light intensities of less than 6.5 candles per sq. ft. remains significant ($P < .001$) after all three environmental factors are taken into consideration. When the light intensity is greater than 6.5 candles per sq. ft., there is no significant regression on either temperature, humidity, or light. The relationship between light and activity (Fig. 10) indicates a wide range of optimum light.

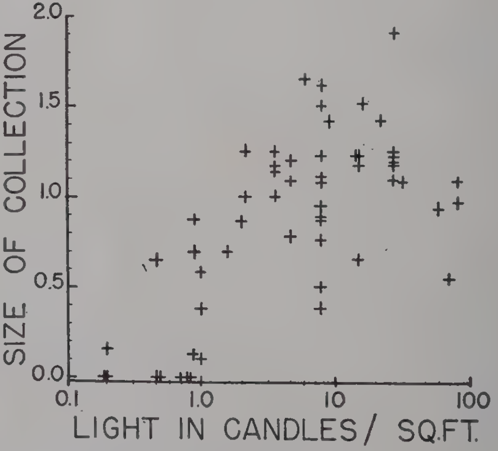

Fig. 10. Afternoon woodland activity of *D. obscura* in relation to light. (Activity measured as in *Fig.* 4.)

The mathematical analysis of the morning collection data shows a significant regression of activity on light intensity after temperature has been taken into consideration ($P < .01$) and on temperature after light has been taken into consideration ($P < .05$). As in the afternoon, when the light intensity is greater than 6.5 candles per sq. ft., there is no significant regression of activity on either temperature, humidity, or light.

D. OBSCURA: Conclusions

Thus, the general pattern of activity of *D. obscura* appears to be a beginning of flight at dawn, an increase in activity during the morning, as the light intensity and temperature increase; and a cessation of activity at dusk, as the light intensity drops below 6.5 candles per sq. ft. The fluctuations in numbers of flies caught during the day are significant at about the 1% level, and may be due to exposure of the cups to direct sunlight, or to some other factor which was not measured.

Discussion

Evidence presented in this paper indicates that the activity pattern of *D. subobscura* may be interpreted as the result of direct response to environmental conditions of light (during the summer) and temperature (during the winter). It is, however, not possible, from a correlation between activity and environmental conditions, to establish with certainty a "cause and effect" relationship, and laboratory experiments are needed to confirm the hypotheses put forward in this paper.

From data similar to that presented in this paper, together with very meager experimental data, Pavan, Dobzhansky and Burla (1950) have stated that the diurnal periodicity found in certain species of Drosophila is "an adaptation to humidity and temperature conditions in the environment . . . (even if) . . . it is not evoked by humidity and temperature changes." (*i.e.* that although in certain instances light is the environmental cue to which the flies are responding, it is, in fact, environmental temperature and humidity which are critical). Since field data could not differentiate between the situation where light intensity is the cue, and environmental temperature and humidity the critical factors, and the situation where light intensity itself is the critical factor, the acceptance of the above conclusion without further experimentation is open to criticism. The adaptive nature of the diurnal cycle of Drosophila, and the factors to which it is an adaptation, seem to remain a question which can be settled only by laboratory studies.

Summary

D. subobscura and *D. obscura* (closely related species which can be found in large numbers in the same woodland) show quite different patterns of daily activity. This difference in activity pattern appears to be related to a difference in response to light (see Figs. 4 and 10).

D. subobscura in the summer invariably has a marked peak of activity in the evening, usually a peak of activity in the morning, and little or no activity in the middle of the day. This behavior is highly correlated with light intensity, for the activity drops sharply at light intensities below and above 6.5 candles per sq. ft. In the evening, no effect of temperature can be detected, either in the woodland or meadow collections; in the morning, however, both light intensity and temperature appear to be important. This would explain the lower and later morning peak of activity found in most of the collections I made in England. In the early spring and late autumn (when temperatures are usually below 15°C) the activity appears to be primarily dependent on temperature, increasing as the temperature rises, and the light intensity has only a subsidiary influence.

D. obscura has a quite different pattern of summer activity. The flies begin to be active as it becomes light; activity increases as temperature and light intensity increase during the early morning, and ceases as it becomes dark.

Thus, it seems that *D. obscura* is responding to low light intensity and to low temperature, but has a wide range of tolerance of both light and temperature. *D. subobscura,* on the other hand, appears to respond to low, and possibly high, temperatures, but primarily to have a very definite light optimum.

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ENVIRONMENTAL FACTORS AFFECTING DISTRIBUTION OF MAYFLY NYMPHS IN DOUGLAS LAKE, MICHIGAN

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Introduction

Most information of an ecological nature dealing with mayflies of lakes is scattered among numerous publications on bottom fauna studies (Muttkowski 1918; Baker 1918; Adamstone 1924; Rawson 1930; Neave 1932, 1934; Berg 1938). In such studies the mayflies are usually treated as an order or as genera and but rarely are specific identifications or specific information given. Also, brief notes on mayfly nymphal distribution which have been made by collectors from incidental observations are often included in taxonomic accounts. A wealth of ecological data is contained in Berner's (1950) publication on Florida mayflies. Ide (1935) has demonstrated clearly the effect of temperature on the logitudinal distribution of mayflies in a stream. Linduska (1942) has shown that the type of bottom in streams is an important factor influencing the local distribution of mayfly nymphs. Up to the present time no intensive ecological study of the mayfly fauna of any one North American lake as a whole has been undertaken. Relatively little is known concerning the environmental factors governing the distribution of immature stages of mayflies within lakes. The present study was made in an effort to ascertain the distribution pattern of all species of mayfly nymphs in Douglas Lake, Cheboygan County, Michigan, and to discover the environmental factors influencing this distribution. The work was conducted during four summers, 1936-1939, supplemented by late-spring and early-fall observations. A description of methods used in this work has been discussed previously (Lyman 1955).

Description of Habitats

Since other authors (Scott 1921; Welch 1928; Eggleton 1931; Moffett 1943) have adequately described limnological characteristics for Douglas Lake, it is unnecessary to repeat a general description of this lake; therefore, only significant habitat details applicable to this study are given.

The littoral region of Douglas Lake (Fig. 1) is primarily sand intermixed with varying amounts of marl depending upon the degree of protection of the particular situation. Prevailing winds blow from a northwesterly direction along the four-mile major axis of the lake. In protected situations such as Maple and Marl bays, marl is more conspicuous while in larger, exposed bays such as North and South Fishtail, the bays between promontories, such as between Robert's and Stony points, or in Nutting's Bay, sand is distinctly predominant and marl is almost absent, especially in the shallower water near the shore. In these bays *Scirpus americanus* occurs close to shore and *S. occidentalis* in the deeper water. West of Fairy Island is a shallow area covered by *Phragmites communis*. Heavy stands of emergent aquatic plants are conspicuously absent from a large proportion of the littoral zone.

In relatively small especially protected situations occurring only in Maple Bay, Marl Bay, Sedge Point, and Hook Point, a fine, organic detritus is present near shore and ecological conditions typical of ponds are approached. Such habitats are of very limited extent in Douglas Lake. The cove of Hook Point and the Sedge Point pools will serve as descriptive examples of this habitat type.

Hook Point cove is well-protected and free from strong wave action. Immediately behind the point is a shallow, organic detritus bottom which grades gradually into a flocculent marl deposit northward along the west shore. Beneath this flocculent marl is fine sand lying upon a coarser sand and pebbles. Few stones occur in this habitat. Farther north along the west shore the marl bottom is replaced abruptly by almost pure sand. Distinctive of the Hook Point habitat is the large quantity of water-soaked logs and sticks deposited there by currents. Such a collection of wood fragments in shallow water is found in no other place in the lake. Higher aquatic plants are relatively scarce in this situation. Among those present are *Nymphaea advena,* just behind the point, and a few scattered plants of *Scirpus americans, S. occidentalis, Potamogeton compressus,* and *Myriophyllum heterophyllum* on the marl bottom.

On Sedge Point are located three beach pools; two of these are closed to the lake but one is still connected to it by a narrow neck of water. The bottoms are covered with organic detritus and plant fragments. The two younger pools do not dry up although the water in the second becomes very shallow by the end of August.

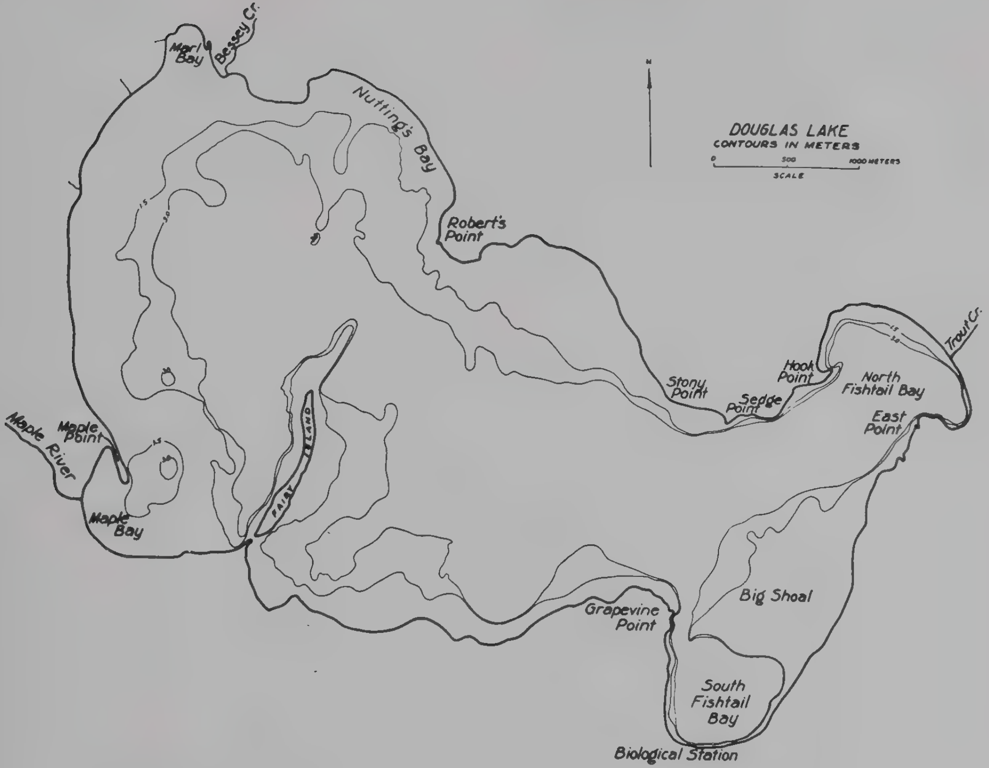
Marl Bay
Bessey Cr.
Nutting's Bay
N
DOUGLAS LAKE
CONTOURS IN METERS
0
500
1000 METERS
SCALE
Robert's Point
Trout Cr.
Hook Point
North Fishtail Bay
Stony Point
Sedge Point
East Point
Maple River
Maple Point
Maple Bay
FAIRY ISLAND
Big Shoal
Grapevine Point
South Fishtail Bay
Biological Station

FIG. 1. Map of Douglas Lake, Cheboygan County, Michigan. Contours at 1.5 and 3.0 meters.

The promontories or headlands such as the northeast end of Fairy Island, Grapevine Point, Stony Point, and Robert's Point are gravelly to rocky. For the most part the stones are located in a narrow strip close to shore and do not extend lakeward to the edge of the submerged shelf. These points are all exposed to the sweep of the wind and are subject to strong wave action. On the other hand, those projections such as Maple Point, Hook Point, and East Point, not exposed to strong wave action, are distinctly sandy with few if any stones.

Grapevine Point is exposed to the full force of the prevailing winds and offers a good example of this habitat type. A submerged shelf about 150 meters wide slopes very gradually to a depth of 1.5 meters and then drops off rapidly into deep water. A stony strip about 30 meters wide occurs along the shore while the remainder of the shelf lakeward is loose sand. Near shore the sand is compacted by marl to a depth of 0.5-1.5 centimeters, thus forming a semi-hard crust over the bottom. East of the point proper there are no exposed rocks. Opposite the middle and around the west side of the point are found the larger stones which vary in size from small pebbles to large rocks 15-25 centimeters in diameter. Most of the stones are flatly rounded to oval. Close to the shore line the rocks are clean while those in 0.6-1.0 meter of water are covered on their upper surfaces by a thick coat of encrusting organisms and marl. Some of the rocks are partly embedded but many rest loosely on the substratum. The rocks are scattered more or less uniformly on the bottom and do not closely contact one another over most of the area. In the Robert's Point, Stony Point, and northwest Fairy Island areas the stones are of more uniform size, more numerous, and in close contact with one another, otherwise, these areas are similar to the Grapevine Point habitat.

FACTORS INFLUENCING BENTHIC DISTRIBUTION

Most species of mayfly nymphs in Douglas Lake occupy more or less definite habitats because of the influence of environmental factors which operate in varying degrees within different ecological niches occurring in this lake. In one situation is found a comparatively large number of species while in another, only one species occurs, and in some habitats none may be found. In some cases a single factor can be designated as being the one most influential in causing a particular species to select a definite kind of habitat but in other instances it seems rather to be a number of environmental factors operating simultaneously which lead the nymphs to choose one set of conditions to the exclusion of others. No species is ubiquitous over the entire littoral zone but some approach this condition more than others. The following discussion deals with those environmental factors which cause the various species of mayfly nymphs of Douglas Lake to select a particular set of environmental influences.

Physical character of the bottom

Rocks.—The physical character of the bottom is a factor of no small importance governing the distribution of mayfly nymphs. Its significance in streams has been emphasized by Linduska (1942). In those situations characterized by gravelly and rocky bottoms are found one-third of all the species of mayfly nymphs occurring in the lake. Some of these species, viz., *Stenonema interpunctatum, Heptagenia lucidipennis, Ephemerella bicolor, Baetis phoebus,* and *Cloeon rubropictum,* are found only on rocky bottoms; while others, *Stenonema femoratum, Ephemerella temporalis,* and *Ephemerella lutulenta,* although characteristic of stony bottoms, do occur to some extent in other situations.

All of these species possess a strong, positive thigmotactic response which causes them to seek a hold on rocks as a stable, physical support. Both Wodsedalek (1912) and Berner (1950) have commented on this thigmotactic response in *Stenonema* nymphs. When nymphs of *S. femoratum, S. interpunctatum, Ephemerella temporalis, E. lutulenta,* or *E. bicolor* are placed in a vessel of water without a rock, they tend to form clumps by clinging to one another. However, as soon as a rock is placed in the water, they immediately release their hold on one another and swim to it. The tenacity with which they cling is well-illustrated by the fact that if an attempt is made to detach them from the rock, they will often allow a leg to be torn from the body before releasing their hold. These nymphs have very little swimming ability but they are agile runners which is another reason for their association with rocks. *Stenonema femoratum* and *S. interpunctatum* nymphs seem to prefer to live ventral side uppermost which can readily be accomplished on a rocky bottom (Lyman 1945).

The reactions of *Cloeon rubropictum* and *Baetis phoebus* to rocks are illustrated by placing these nymphs in a dish of water without a rock. They make no attempt to gather in clumps but show a decided restlessness by swimming with rapid spurts here and there and finally become distributed around the periphery of the container. When a stone is introduced into the center of the dish, it barely comes to rest before the nymphs begin swimming toward it from all sides. Even when a rock is held over the dish just out of the water, the nymphs will follow it as it is moved from one end of the dish to the other. These two species are strong and rapid swimmers for short distances. However, they lack the ability to keep up sustained swimming movements for any considerable length of time. Rocks, therefore, offer these nymphs a solid support upon which they can move rapidly without the necessity of sustained swimming efforts. The tenaciousness of all these clinging nymphs is well-shown by the fact that they rarely release their hold when a rock is lifted off the substratum, or even entirely out of the water.

The relative proximity of rocks to one another seems to determine to some degree the distribution of *Heptagenia lucidipennis.* These nymphs are found on Fairy Island, Stony Point, and Robert's Point where rocks occur closer together than on Grapevine Point. This same type of distribution was also found in nearby Burt Lake where similar habitats occur. Indications are that *Stenonema interpunctatum* is also influenced to a lesser degree by the proximity of rocks since these nymphs are found only in distinctly rocky habitats and, unlike *S. femoratum,* they are not found under isolated stones scattered over predominantly sandy areas.

The degree of burial of the rocks in the substratum is important since practically all nymphs which live on rocks choose the under side and do not occur on those that have the lower surface wholly embedded in the bottom.

In the case of *S. interpunctatum* the water depth to which rocks occur is apparently significant for they are more generally found on those rocks in deeper water. In the Stony Point situation where rocks occur only near the shore line very few of these nymphs were ever found yet *S. femoratum* was very common.

The specific gravity of rocks as contrasted to that of wood tends to aid in maintaining the position of rocks on the bottom in the face of strong wave action. Wood, because of its comparatively light weight, is readily eliminated as a possible shelter or stable support for nymphs along a wave-swept shore since it is easily transported by wave action and is usually deposited above the waterline. In a marly or an organic-detritus habitat, rocks are eliminated because they tend to settle and eventually become buried in the deposit.

Sand.—Along the open, sandy beaches practically no mayflies are found in shallow water (0.0-1.5 meters). Sand bottoms are distinctly rejected by mayfly nymphs in preference to other kinds when such nymphs have the opportunity of selecting various bottoms. In the case of clinging forms, sand offers them no means of solid, physical support as it is almost impossible for these nymphs to secure a strong hold on loose sand grains which are readily displaced by the curved claws with each attempt to move. Burrowing forms, such as *Hexagenia limbata,* and probably *Ephemera simulans,* find that a sandy substratum offers too much physical resistance to burrowing for it is is easily demonstrated that clean sand grains tend to settle back into any depression as it is dug by the nymphs (Lyman 1943).

Marl.—The extensive marl-bottom regions of Maple and Marl Bays support few, if any, species of mayfly nymphs. Such a bottom offers no more attraction to clinging forms than does a sand bottom for reasons already stated. Very few burrowing mayflies were found in this type of bottom even though they do have the ability to burrow into it.

Mud.—Mud bottoms are restricted to the sublittoral and profundal regions of Douglas Lake. The only mayflies that inhabit the sublittoral muds are *Hexagenia limbata* and *Hexagenia affiliata.* Mud offers these nymphs a distinctly favorable burrowing medium for which they are adapted both morphologically and physiologically (Lyman 1943; Hunt 1953).

Organic Detritus.—In habitats where organic detritus prevails *Caenis simulans* nymphs are abundant and in some places *Brachycercus lacustris, Ephemerella temporalis, E. lutulenta,* and *Leptophlebia nebulosa* occur in lesser numbers along with them.

On detritus bottoms the sprawling and slow-moving nymphs of *C. simulans* escape detection by partially settling into the surface of the detritus and become almost invisible due to detritus particles which collect on the setae of the body. They are particularly adapted for a detritus environment since the second gill is modified to form a gill-cover which is used for protection and to maintain the gills free of detritus particles (Eastham 1936). Detritus bottoms are rich in microorganisms and organic material which furnishes abundant food for the nymphs. That a detritus substratum rich in organic matter is selected by the nymphs in preference to a more distinctly marl bottom is indicated by the Hook Point, Marl Bay, and Maple Bay situations where marl and detritus bottoms occur side by side, each being more or less distinct from the other. On the detritus bottom are found numerous *C. simulans* nymphs but on the marly bottom a short distance away comparatively few of these nymphs occur.

While *C. simulans* and *E. temporalis* possess the ability to cling to objects, as is evidenced by their association with rocks or the stems of submerged plants, they seem to be limited to those situations where organic debris is prevalent as a constituent of the substratum. Their presence in plant beds is probably due to the organic detritus which collects in these areas.

Wave action

Wave action is one of the principal environmental factors affecting either directly or indirectly the distribution of mayfly nymphs in Douglas Lake. The majority of lake species are inhabitants of the shallow littoral regions. Therefore, they must either seek those situations in which wave action is much reduced or find some means of protecting themselves while living under the rigorous conditions produced by wave action.

Along open sandy beaches, severe wave action results in the sand being shifted from one place to another thus producing molar action and a very dynamic environment with which mayfly nymphs are unable to cope. It is readily conceivable that molar action plays a major part in destroying mayfly eggs which may be deposited on the loose sand of these areas by grinding them to pieces or burying them in such a way as to make it impossible for those nymphs which hatch and have no burrowing ability to reach the surface of the sand.

Mayflies characteristic of lakes do not live in a wave-swept, sandy situation because they are carried by water movements from one place to another, since the sandy substratum offers no means of stable, physical support to which they can cling nor can they maintain their position by swimming. That nymphs are readily carried about by water movements appears to be indicated by the fact that in the spring and autumn some *Caenis simulans* nymphs occur on rocks near the shore line as a result of being carried shoreward from the deeper waters owing to increased wave action during those seasons of the year. Ordinarily nymphs of this species live in ponded situations or at depths below effective wave action.

Experiments were conducted to demonstrate whether mayfly nymphs could live if rocks were provided in an area of sandy bottom subject to very strong wave action but ordinarily containing no rocks. A section of Big Shoal was selected where no rocks were present and from which mayfly nymphs were absent. On May 30 clean rocks collected from land were placed in two piles in about one meter of water on the selected area. No nymphs were found under these rocks on either June 23 or on July 4; however, on August 4 nymphs of *Stenonema femoratum* were found with all sizes present from recently hatched to fully mature. The very small nymphs were most numerous and had probably come from eggs deposited earlier in the summer. On the other hand the mature nymphs had probably been carried in by wave action from another part of the lake and had sought shelter under the only available objects. No other species of nymphs were found on or under the rocks. By August 4 a number of the rocks had already become partially covered by shifting sand and by the following summer the rock piles were almost completely buried and no nymphs could be found. Thus, *S. femoratum* could exist on Big Shoal so long as the rocks were available but disappeared as the rocks became covered by the shifting sands. These nymphs also occurred on isolated rocks in other wave-swept portions of the lake.

The distribution of *Caenis simulans* nymphs at depths of about 1-3 meters around most of the lake seems to be a direct result of the influence of wave action, for in situations where wave action is reduced they occur in shallower water. Under conditions of vigorous wave action in the open portions of the lake *C. simulans* could not exist because of molar action, lack of organic detritus, and water movements. It seems that *C. simulans* has selected a depth below the effective wave-action level (Moffett 1943) and where a fine detritus deposit is also found.

In a habitat such as Hook Point, reduced wave action appears to be one of the principal reasons why *Choroterpes basalis* is common there and absent from a situation like Grapevine Point. This conclusion is also substantiated by observations on other lakes where *C. basalis* is found only in places similar to that prevailing at Hook Point.

In wave-swept areas such as Grapevine Point or Fairy Island, rocks form a stable environment by offering the clinging type of mayfly nymph a means of protecting itself from the force of the waves. Rocks resting on the substratum produce recesses into which the nymphs can retire where molar action and water movements are reduced to a marked degree.

Light

Light is an important environmental factor that plays a major role in influencing the distribution of mayfly nymphs. Both species of *Stenonema* are definitely limited in their distribution to those habitats where rocks are present because they react negatively to light, seeking the under side of rocks during the day and moving to the upper surface only at night (Lyman 1945). *Heptagenia lucidipennis, Leptophlebia nebulosa, Choroterpes basalis, Ephemerella temporalis, E. lutulenta, E. bicolor,* and *Caenis simulans* also appear to be negatively phototactic, since in the natural environment they all select situations where the light intensity is much reduced. It seems that the factor of light alone is sufficient to eliminate these mayflies from open, sandy, or marly areas since these situations offer non-burrowing forms no means of protection from light. *Choroterpes basalis,* for example, seems to show a distinct preference for marl bottoms but does not occur in Marl or Maple Bays. One of the reasons for this fact appears to be the influence of light. At Hook Point and similar habitats in other lakes, *C. basalis* is found only on marly bottoms where wood fragments are present. The under side of wood offers these nymphs a refuge from light during the day. In Marl and Maple Bays practically no wood fragments are found.

Other factors

Emergent plants furnish mayflies, such as *Ephemerella temporalis* and *Caenis simulans,* physical support, shelter and, indirectly, food. In some places these plants aid in reducing the force of wave action and allow finely divided debris to collect on the bottom. *Siphloplecton basale* nymphs were often found in beds of *Scirpus* near the shore where they appeared to congregate for temporary shelter during their shoreward migration just prior to emergence. No species of mayfly nymphs were discovered which were wholly limited to emergent plant zones and those found there appeared to be transients.

The part played by submerged plants as a habitat for mayfly nymphs is probably an important one although little is known concerning it. Krecker (1939) pointed out that in Lake Erie *Myriophyllum spicatum* has the largest population of mayfly nymphs. Since certain species of nymphs were found nowhere else in the lake, it is concluded that they (*Siphloplecton basale, Tricorythodes allectus, Centroptilum fragile,* and *Pseudocloeon dubium*) are undoubtedly limited to the submerged plant zone.

Water level changes markedly affect the distribution of certain species of mayfly nymphs. In the early spring the high water results in the formation of many shore pools into which *Leptophlebia nebulosa, Siphlonurus rapidus,* and in some instances *Ephemerella temporalis* and *E. lutulenta* migrate. As the water level drops during the summer months, many rocks become exposed to the air and are thus eliminated as habitats for those mayflies which normally depend upon them. *Stenonema interpunctatum* which tends to select rocks in deeper water and not those near the shore line probably does not occur at Stony Point for the reason that the drop in water level exposes most of the rocky area leaving but few rocks under water near the shore line.

According to Ide (1935) water temperature is an important factor influencing distribution of mayfly nymphs in a stream. On the contrary, it appears to have but small effect upon the distribution of these insects in a lake since there is a tendency toward temperature uniformity at any given time over the entire littoral region. The only instance in which temperature seemed to be a factor is in the early spring when *Leptophlebia nebulosa* and *Siphlonurus rapidus* migrate into the very shallow water of shore pools. This migration may be a temperature response since the shallow, quiet water of these pools warms faster than does the water of the lake. Neave (1930) has pointed out that in the case of *Blasturus cupidus* (= *Leptophlebia cupida*) the spring "migration is due to an internal instinct." He also stated that the amount and kind of food probably causes the nymphs to seek a new habitat in the spring.

Dissolved oxygen, like temperature, tends toward uniformity at any given time over the entire littoral area and appears to have little if any effect upon distribution of mayfly nymphs. However, in the case of *Hexagenia* nymphs it seems to limit their distribution in Douglas Lake to a maximum depth of about 15 meters. Physicochemical studies on this lake (Welch 1928; Welch and Eggleton 1932, 1935) have shown that beyond this level the amount of dissolved oxygen drops off rapidly. In a recent paper Britt (1955) has shown that *Hexagenia* nymphs in Lake Erie could not survive conditions of low oxygen (0.7 p.p.m.).

DISCUSSION

The mayfly nymphs in Douglas Lake form a definite distribution pattern because of the influence of certain environmental factors that operate simultaneously in each of the more or less distinct habitats. The importance of the interaction of environmental factors should not be overlooked since often the consideration of a single factor alone is not a sufficient criterion to determine the presence or absence of nymphs within a given environment. *Choroterpes basalis*, for example, is restricted to a relatively small area in the vicinity of Hook Point. The principal environmental influences which have led these nymphs to select such a habitat in preference to all others appear to be: (1) a predominantly marl bottom, (2) absence of strong wave action, and (3) presence of wood fragments which afford shelter from light. Grapevine Point offers rocks which afford a shelter from light and which are covered with encrusting organisms and marl that the nymphs eat very readily, yet the presence of strong wave action seems enough to preclude *C. basalis* nymphs from this situation. Marl and Maple Bays have distinct marl bottoms and there is little wave action, but the almost total absence of wood fragments seems sufficient reason for the absence of the nymphs from those areas. In Florida, Berner (1950) found *Choroterpes hubbelli* definitely associated with wood and leaves.

The exclusion of all species of mayfly nymphs from the extensive, shallow, sandy shoal areas (less than one meter depth) of Douglas Lake is due to several factors, and almost any one of them appears to be adequate reason for their absence. This environment presents no means by which non-burrowing forms can obtain shelter from light, wave action, and molar action. Burrowing nymphs find that sand is too difficult a medium for digging. Clinging forms cannot maintain their position on the easily shifted sand grains which afford them no firm physical support. Berner (1950) found mayfly nymphs on sandy lake shoals only when other physical supports such as wood or rocks were present.

Below the level of effective wave action (1-2 meters) on more or less open bottoms adjacent to the shallow, sandy shoal environment is a region where *Caenis simulans* and *Brachycercus lacustris* nymphs occur. While the substratum here is essentially sandy, there are also present varying amounts of organic detritus and flocculent marl that provide these sprawling nymphs with a favorable medium in which to live. The clinging response, while present does not appear to be nearly so strong in these nymphs as in such forms as *Stenonema femoratum*, *S. interpunctatum*, *Heptagenia lucidipennis*, and others. This reaction alone accounts for the absence of the latter nymphs. *Caenis simulans* and *Brachycercus lacustris* are both adapted with a modified gill for keeping the gills free from the debris. *Ephemerella* nymphs also have modified gills which probably serve the same function; however, these nymphs are found but rarely in the situation under discussion. The thigmotactic response seems to play its part as a factor in the distribution pattern as displayed by the *Ephemerella* nymphs in rocky situations but *E. temporalis* and *E. lutulenta* were also found in such places as Hook Point and one of the pools on Sedge Point where organic detritus is prominent. In these latter places, however, the nymphs were usually found clinging to such objects as wood fragments or old decaying plant stems and occurred infrequently sprawled in the finely divided detritus on the bottom. Even though these nymphs, like those of *Caenis simulans,* are morphologically adapted for living on an organic detritus bottom, the relative strength of their clinging propensities seems to afford two of them (*E. temporalis* and *E. lutulenta*) a wider range of adaptability but limits the third (*E. bicolor*).

The suitability of the rocky habitats for mayfly nymphs in Douglas Lake is well proven by the relatively large number of species that occur in those situations. The Heptageniinae species of Douglas Lake are particularly adapted to this environment and form the bulk of the mayfly population. They are flattened dorso-ventrally, have a strong, positive, thigmotactic response, possess the ability to move with rapidity over the surface of rocks, are negative to light, and prefer to live ventral side uppermost. The requirements of all these adaptations are met by a rocky habitat. Probably the most important single environmental factor which limits these nymphs to rocks is their strong, negative reaction to light. Wave action appears to be more of an indirect influence since all of these nymphs can live in standing water. *Stenonema femoratum* often occurs in many of the quiet water situations around the lake wherever shelter is available. *Heptagenia lucidipennis* and *Stenonema interpunctatum* are more limited in their distribution than *S. femoratum* since they seem to require situations where the rocks are relatively close to one another. In this respect *H. lucidipennis* reacts more strongly than does *S. interpunctatum* since the former is limited to rocky areas as provided by Fairy Island, Stony Point, and Robert's Point. In contrast to the sandy shoal environments the rocky areas of Douglas Lake are more stabilized. Rocks furnish a solid, physical support. The encrusting organisms which cover the rocks furnish plentiful food. All nymphs characteristic of rocky situations possess a strong clinging response which appears similar in importance to the light reaction.

OUTLINE OF HABITAT DISTRIBUTION PATTERN AS DISPLAYED BY DOUGLAS LAKE MAYFLIES

I. Littoral
  A. Beach pools
    1. Temporary
      Siphlonurus rapidus (c)
      Leptophlebia nebulosa (c)
      Ephemerella lutulenta (c)
      Ephemerella temporalis (c)
      Caenis simulans (c)
    2. Permanent
      Ephemerella lutulenta (c)
      Ephemerella temporalis (c)
      Caenis simulans (a)
      Callibaetis ferrugineus (r)
  B. Rocks
    1. Near shore line
      Baetis phoebus
    2. Shallow water
      a. Close together
        Stenonema femoratum (a)
        Stenonema interpunctatum (r)
        Heptagenia lucidipennis (a)
        Ephemerella bicolor (a)
        Ephemerella lutulenta (c)
        Ephemerella temporalis (c)
      b. Scattered
        Stenonema femoratum (c)
        Cloeon rubropictum (s)
  C. Sand
    1. Wave-swept
      Siphloplecton basale (when emerging)
    2. Below effective wave action
      Ephemera simulans (s)
      Hexagenia limbata (r)
      Hexagenia affiliata (?)
      Baetisca obesa (r)
      Brachycercus lacustris (s)
      Caenis simulans (a)
  D. Marl
    1. Wood fragments absent
      Caenis simulans (s)
    2. Wood fragments present
      Stenonema femoratum (c)
      Choroterpes basalis (a)
      Ephemerella lutulenta (c)
      Ephemerella temporalis (c)
      Caenis simulans (s)
  E. Organic detritus
      Leptophlebia nebulosa (c)
      Ephemerella temporalis (c)
      Ephemerella lutulenta (c)
      Caenis simulans (a)
  F. Emergent plant zone
      Siphloplecton basale (when emerging)
      Caenis simulans (s)
      Ephemerella lutulenta (c)
      Ephemerella temporalis (s)
      Ephemerella bicolor (s)
II. Sublittoral
  A. Submerged plant zone
      Siphloplecton basale (?)
      Tricorythodes allectus (?)
      Caenis simulans (c)
      Centroptilum fragile (?)
      Pseudocloeon dubium (?)

B. Mud
  Hexagenia limbata (a)
  Hexagenia affiliata (?)

III. Profundal (all forms absent)
Symbols: (a) abundant; (c) common; (s) scarce; (r) rare; (?) relative abundance unknown but probably occur in habitat indicated.

Mayfly Productivity of Douglas Lake

While this study involved little attempt at the quantitative approach to mayfly productivity in Douglas Lake, certain conclusions may be reached chiefly from observational data. From the standpoint of both quantity and quality, mayfly productivity in Douglas Lake may be considered low. The principal reason for this is apparent when the relative proportions of those areas which are productive or unproductive of nymphs are contrasted. As has already been pointed out, the wave-swept, sandy shoal regions of Douglas Lake are extensive as compared to those which are rocky or protected from strong wave action. Mayflies occur primarily in the latter situations; consequently, only about 15 per cent of the total area of lake bottom included by the 0- and 3-meter contours supports a mayfly population. It is also significant that the majority of the rocks in the lake are located close to the shore line and many become exposed to the air each year during the period of low water level. The usual drop in water level is about 0.6 meter, and since the slope of bottom in the littoral region is very gradual, a considerable proportion of this area is exposed in late summer. It is very probable that the lowered water level has marked effect upon the population of mayfly nymphs; and if the water level were maintained at a higher point than at present, the mayfly production of the lake as a whole would probably be increased.

The region of Douglas Lake which is most productive of *Hexagenia* is included within the 9 and 15 meter contours and comprises only about 15 per cent of the entire lake bottom. In lakes where the density of *Hexagenia* is high a large proportion of the bottom in deep water is available as a habitat for these nymphs, a condition not true of Douglas Lake. In the latter, about 85 per cent of the lake bottom is unsuitable for *Hexagenia* nymphs because of its sandy character or because of lack of sufficient dissolved oxygen due to thermocline formation in the several individual depressions.

Summary

This investigation is the first intensive study of the mayfly fauna of a North American lake in which the primary purpose was to determine the local distributional pattern of the nymphs together with the environmental factors responsible for it. It was found that the physical character of the bottom, light intensity, and wave action are the principal factors which interact to determine the distributional patterns. The positive thigmotactic response of certain species of nymphs is also an important influence in distribution and accounts for the absence of nymphs from habitats lacking physical support. Temperature and dissolved oxygen have little, if any, effect on nymphal distribution within lakes. However, *Hexagenia* nymphs are limited by oxygen to that portion of the mud bottom above the hypolimnion. Low mayfly productivity in Douglas Lake arises from the fact that only about 15 per cent of the total bottom area is suitable for mayfly populations.

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A STUDY OF A CALANOID COPEPOD POPULATION IN AN ARCTIC LAKE[1]

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Introduction

The purpose of this paper is to describe the cyclical activities of a calanoid copepod, *Limnocalanus johanseni,* in an arctic lake. This lake, called "Imikpuk" by the Eskimos, is a small, shallow, fresh-water body located on the arctic coast of the northernmost tip of Alaska at Point Barrow. The fauna supported by Imikpuk was surprisingly varied. Among the more conspicuous organisms present was the little-known copepod *Limnocalanus johanseni* Marsh; rotifers of the genera *Kellicottia, Synchaeta, Notholca,* and *Keratella; Cyclops scutifer* Sars; and a cladoceran *Daphnia pulex* var. *tenebrosa* Sars, which was conspicuous because of its large size as well as abundance. Occurring in the plankton, but not in excessive numbers, were two species of Anostraca, at least one species of the Notostracan, *Apus,* and occasionally specimens of a second little-known calanoid, *Eurytemora canadensis* Marsh. In one collection only were found two specimens of the calanoids *Diaptomus glacialis* Sars and *Diaptomus alaskaensis* M. S. Wilson.

The field work was done during the summer of 1952 between July 10 and September 27, and the sample counting was done during the fall of the same year. The Arctic Research Laboratory at Point Barrow was the base from which all the field work was done, and its laboratory facilities were adequate to make very frequent determinations of soluble phosphorus, total nitrogen, and chlorophyll, as well as other routine analyses which included oxygen, pH, alkalinity, and the physical measurements of temperature, transparency, and total suspended material (seston). The photosynthetic activity of the lake was also studied during this summer (Comita and Edmondson 1953). Sufficient data were taken so that the heat budget could be computed and seasonal activities of several plankters outlined in addition to those of the copepod being presented at this time. A discussion of these data is in preparation.

During the course of the present work, I have received a great deal of help from many persons to whom I owe a heavy debt of gratitude. Professor W. T. Edmondson has given advice and guidance not only in the planning but also in the execution of the over-all project for which he was principal investigator. Dr. I. L. Wiggins took the April 1953 samples and kindly placed the facilities of the Arctic Research Laboratory at my disposal. John J. Koranda took seven plankton hauls from Imikpuk after it had frozen over in the fall of 1952.

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[1] Part of a thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy at the University of Washington, Seattle, Washington.

These collections made it possible to assess certain facts in connection with the biology of the *Limnocalanus* population. Much of the temperature data were taken from thermistor cable #180 in Imikpuk and kindly furnished by Max C. Brewer and the United States Geological Survey. Prof. D. Chapman offered important advice on various matters concerning the statistical treatment of the data. Jean J. Comita helped me very greatly in nearly all phases of the work, in the field as well as on the manuscript.

Those that helped in the identification of the organisms are: M. S. Wilson, calanoids; J. L. Brooks, Cladocera; W. T. Edmondson, rotifers.

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The Lake

Imikpuk is one of the oriented lakes of the Arctic Coastal Plains Province of Alaska. It is not as strongly oriented as are the neighboring lakes further south in this province. Its longest axis is on a line approximately 11° east of true north. Since many of the lakes are oriented west of true north, N 9°W to N 21°W (Black and Barksdale 1949), Imikpuk does not conform to the general pattern of orientation. It appears to be aligned more or less in the direction of the present prevailing winds.

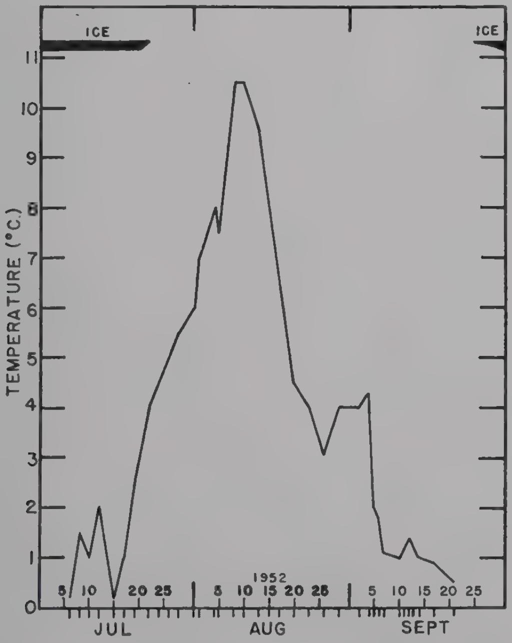

FIG. 1. Temperature curve for Imikpuk during the summer of 1952. Dates on which temperatures were taken indicated below the x-axis are: July 6, 8, 10, 12, 15, 17, 19, 22, 24, 26, 28, 31; August 1, 4, 5, 8, 10, 13, 15, 17, 20, 23, 26, 29; September 2, 4, 5, 6, 7, 10, 11, 12, 13, 14, 17, 21.

The lake is elliptical in outline, has an area of 61 hectares, a mean depth of 2.1 meters, and is completely underlain by permafrost. Most of its bottom is hard frozen silt except in its deepest part (2.8 meters), where it has several feet of soft mud. The shape of the lake is such that winds disturb it easily, and since in the arctic climate daily steady winds are usual, there was no stratification. The low rainfall makes this area essentially an arctic desert.

Since this lake is in an arctic climate its temperature cycle (Fig. 1) is exceedingly compressed. In 1952 it became warmer at the rate of 0.3°C per day. Its maximum temperature of 10.5°C was maintained for only three days after which it rapidly dropped to freezing again. Temperature measurements were taken daily by means of a Centigrade thermometer at the water surface, but thermal profiles of the entire water column were available from August 26 until December 2. They were taken from a thermistor cable operated by the U. S. Geological Survey as part of its investigation of the permafrost. The thermistors on this cable were placed at 12 inch levels, which was close enough to indicate any stratification in the lake during the summer.

The lake was free of ice only 65 days in 1952.

The water in Imikpuk was soft; its pH through the summer of 1952 was about 7.5, and there was evidence (Prescott 1952) that it was below 7 through the previous winter. Alkalinity measurements (as HCO_3) were low throughout the sampling time, ranging from 15.2 (6 July 52) to 23.2 ppm (17 Sept 52).

A sparse fringe of grasses was noted in small sheltered indentations on the eastern shore where the lake was connected to the Arctic Ocean through a shallow lagoon and a very shallow marsh, and on the southern shore where there was a small, slightly protected marsh. The latter had a variety of small submerged and emergent aquatic plants. The bottom had mats of *Vaucheria* in thick clumps between the center of the lake and the shore, but these became sparse near shore.

As far as is known there were no fish in the lake; hence, the analysis of population fluctuations is relatively more simple than it is in lakes where fish predators are present.

METHODS

The plankton was taken by means of the Clarke-Bumpus closing-type plankton sampler. Early in the sampling period plankton hauls were made daily. Later this interval was increased to four-day periods, but there was some variation in the length of time between collecting dates, the longest time being 5 days between August 15 and 20. The frequency of sampling was such that a reasonably accurate estimate of the duration of the instars was possible. The lake was visited at varying times of the day between 8 a.m. and 5 p.m. local time, but mostly during the morning hours. For this reason it is possible that copepods showing strong diurnal migrations may not have been taken.

On each day of collection samples of the population were taken using #20 bolting silk nets (mean net hole size, 0.07mm^2); at no time was there any indication that the net clogged. Because of the shallow depth (9 ft) it was possible to draw the sampler uniformly by hand from top to bottom of the lake and alternately from bottom to top. The tows were usually made along a course normal to the wind or in a circle in water deep enough to prevent scraping the bottom mud. Since Imikpuk is a small lake, it is considered that it was adequately traversed when the hauls were taken. The number of liters filtered in all the collections varied between 54.7 and 958 (mean 395.7). These samples were not true duplicates since they could not be taken over the exact same course nor were the volumes of water filtered the same for each run. However, since two samples were taken consecutively with the same size net, they are considered as duplicates in the treatment of the data.[2]

No attempt was made to evaluate the shore fauna and flora as such. In many tows the larvae of the notostracan *Apus,* known to live just over the bottom in shallow lakes and ponds, were taken, indicating that the bottom of the water column was sampled frequently.

All samples were counted at the end of the summer. For counting the nauplii three or more one-ml aliquots in Sedgwick-Rafter counting chamber were taken from the raw sample, and identification as well as counting were done simultaneously using a compound microscope. For counting the copepodids the aliquots were increased to three ml each, and counting was done in a small plastic chamber (4 x 4 x ½ cm) using a dissecting microscope.

The population deviation from the mean for the two samples taken on each date was computed as a percentage. The average of these deviations is 8.54 percent of the mean, and the range was from 0.158 to 35.3 per cent. This is a small amount of deviation considered in the light of the usual range in plankton work.

The factor for the sampler was obtained by connecting the sampler to a convenient water outlet. The connections were made using an innertube of a motorcycle tire so fastened that leakage was at a minimum. This was operated at a flow rate of 17.7 gallons per minute (14.6 revolutions per minute) which was the maximum flow the water system could produce. Eleven runs were made and the factor, liters/revolution, was found to vary between 4.22 and 4.74, and the mean of these runs was 4.6 liters/revolution. While this was not an exhaustive test, it is considered to be reasonably good, and it is in agreement with the published computations of Clarke and Bumpus (1950).

Using a more elaborate apparatus at a later date this particular meter was recalibrated at the University of Washington Oceanographic Laboratories by Mr. C. S. Yentsh. His calibration, which was 4.438 liters per revolution at 60 revolutions per minute, checks mine closely even at the higher rate of water flow.

In the analysis of some of the data, acetone extracts of chlorophyll were used as a measure of food supply, although it is recognized that acetone extracts of chlorophyll are not always related to quantity of algae. The acetone extracts of chlorophyll were measured on a Klett-Summerson colorimeter and are therefore called Klett units. Throughout this study the Klett unit is used as a measure to indicate changes in food supply. A rough conversion from Klett units to weight of chlorophyll (a and b) can be made using the following conversion factor: 1 Klett unit/liter = 0.3 micrograms/liter. All other chemical measurements mentioned were made using standard methods (A.P.H.A. 1946; Welch 1948).

The lake was sounded on several days between samplings. This was done by measuring the depth at intervals across definite transects in many different directions over the lake. The contour map drawn from these data is being presented in a separate paper, but the morphometric data are presented in Table I.

TABLE I. Morphometric Data for Imikpuk

Depth (meters)	Area (hectares)	Volume (cubic meters)	Percent Volume
0	61	564,700	45.1
1	52	453,900	36.3
2	39	233,000	18.6
2.8	19	....	....
Total........	....	1,251,600	100.0

Maximum depth 2.8 meters.
Mean depth 2.1 meters.

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[2] The population numbers of all stages of *Limnocalanus johanseni* for the entire season are available by writing the author at the above address.

The weight data on the stage VI nauplii and all stages of copepodids were taken by segregating many individuals of each stage on separate tared coverslips, blotting the preservative from around them as well as possible, and immediately weighing them (wet weight). The animals were then dried at 103°C for about one-half hour and reweighed (dry weight). The younger stages of nauplii were not weighed.

RESULTS AND DISCUSSION

The Life Cycle

The life history of *Limnocalanus johanseni* has been found to consist of six nauplius stages and six copepodid stages in addition to the egg. Each of the stages was recognized by the appearance and state of development of the appendages, as well as the body form. The sixth copepodid stage has been taken to be the definitive adult form, which has been designated as copepodid stage VI or adult. The morphology of the immature stages of copepods has been adequately described; therefore, it is not intended in this paper to present these details. It is hoped that the morphology of the individual stages of this animal will be presented by the author at a later date.

The hatching of *Limnocalanus* in this lake occurred during the melting of the large ice mass that composed about 71 percent of the lake volume at the time of its maximum development. The last remnants of this block of ice were gone on July 22, 1952, but quantitative sampling had already begun on July 10 in the part of the lake that melted earliest.

The duration of each instar was obtained by estimation of the time interval between peaks of each stage as indicated in Table II. The estimated duration time of four days for the first three molts is an uncertain estimation. Wuthrich (1948) noted that in *Diaptomus* (species not indicated, but she was working with the two species *D. gracilis,* and *D. laciniatus*) nauplius stage II appeared one day after stage I, and stage III appeared the fourth day. In the light of the work of Nicholls (1933) and Rees (1949) on *Calanus* it is very probable that stage I nauplius of *Limnocalanus* may have lasted only a few hours, stage II somewhat longer, and stage III as much as 2 days. The duration of nauplius III is probably most like that of nauplius IV so that the duration time for nauplius III was chosen to be equal to that of nauplius IV, which was estimated from the time lapse between projected peaks of the population curves for nauplii IV and V. The duration of instars for the remainder of the larval populations are based on more accurate determinations of peaks for each stage. The equivalent time intervals where known for *Calanus finmarchicus* (Gunn.) given by Nicholls are presented for comparison.

TABLE II. Duration of stages of *Limnocalanus johanseni*

Stage	Time of peak	DURATION OF INSTAR (days)		Mean temperature during interval (°C)
		Limnocalanus johanseni	*Calanus finmarchicus*	
Nauplii:				
I........	? (under ice)	approximately 4 (estimated*)	(–)	1
II........	? " "		(–)	2
III.......	? " "		(–)	1
IV.......	16 July	2	(–)	0.6
V........	18 July	3.5	(–)	1.8
VI.......	21-22 July	5	(–)	3.5
Total..	....	14.5	(11)	
Copepodids:				
I........	26-27 July	3.5	(3)	5.3
II........	30 July	3	(3)	5.8
III.......	2 August	3	(3)	7
IV.......	5 August	5	(3)	7.5
V........	10 August	16	(4)	10.5
VI.......	26 August	120 (estimated)	(42)	3
Total, approximate span of activity....................		165 days		

*Reported previously as 6 days (Comita and Edmondson 1953) but now considered that 4 days is a better estimate.

The samples of July 10 had the first five stages of nauplii present (Fig. 2). At this time stage I

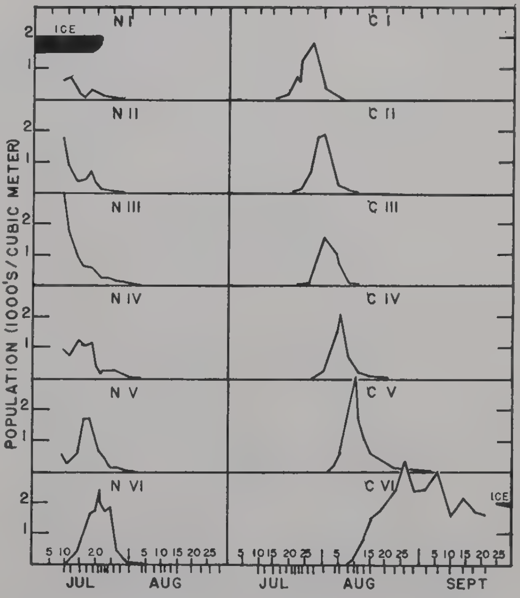

FIG. 2. Numbers of larvae and adults of *L. johanseni* during the summer of 1952. N = nauplius, C = copepodid, CVI = adult. Dates of sampling indicated below the x-axis are: July 10, 12, 15, 17, 19, 21, 22, 23, 24, 26, 28, 31; August 4, 5, 8, 10, 11, 13, 15, 20, 23, 26, 29; September 2, 6, 10, 14, 17, 21.

was well past its peak in numbers and was declining, but it continued to be present until July 26.

Stage II nauplii were found in greater numbers than stage I on July 10, and also on this date stage III were found in still greater numbers than II. Considering the appearance of the curves in Figure 2, even stage III had reached its peak and possibly passed beyond it by that time. Since these three nauplius stages are short-lived their curves drawn from these data are of no help in the determination of their duration. Stages IV, V, and VI followed rapidly and by August 4 all *Limnocalanus* nauplii had disappeared.

Copepodids of stage I (CI, Fig. 2) first appeared seven days before the ice melted completely, passed through their peak between July 26 and 27, and disappeared just after August 5. The next two copepodids followed in succession. Copepodids IV, V, and VI (adults) followed and the last molt required about 16 days for completion as indicated by the 16-day interval between the two peaks in the sample population.

The first adults appeared on August 10, the date of peak numbers of stage V, passed through their peak on August 26, and then began to diminish.

In Table III are listed the periods during which each instar was noted in the samples beginning with nauplius stage VI which was the only nauplius not present in the first samples taken.

TABLE III. Duration of instars. First and last days noted in samples

Stage	Date	Days
N VI	12 July to 31 July	20
C I	17 July to 5 August	20
C II	23 July to 8 August	17
C III	26 July to 10 August	16
C IV	31 July to 15 August	16
C V	4 August to 2 September	30
C VI (Adults)	10 August	—

Since the tail of the curve for the copepodids of stage V may have been composed entirely of males only or females only due to a different molting rate for the two sexes, the composition of the C V's and the C VI's was investigated by examining their sex ratios for each date of their existence. The ratio of males to females (m/f) for each date is presented in Table IV. This ratio deviated very little from one for both stages, indicating that the molting rate for both sexes was the same. It is realized, however, that the ratios of the C VI's may have been affected somewhat by a difference in the mortality of the two sexes. From the ratios it appears that more males failed to molt successfully than females.

TABLE IV. Sex ratios for Copepodids V and VI (adult) populations

Date	C V		C VI	
	Ratio (m/f)	Mean population males & females	Ratio (m/f)	Mean population males & females
4 August	1.08	226.5	....	....
5 August	1.02	508	....	....
8 August	0.98	2008	....	none
10 August	1.13	3134	0.75	198.5
11 August	0.85	1742.5	0.82	602.5
13 August	0.86	1123	0.56	806.5
15 August	1.29	597.5	0.95	1418.5
20 August	1.32	276	1.16	1898
23 August	1.02	96	1.22	2340.5
26 August	3.03	70.5	0.93	3159.5
29 August	0.98	39.5	1.08	2342
2 September	....	none	1.18	2435
6 September	....	....	1.03	3036
10 September	....	....	1.25	1625
14 September	....	....	1.19	2130
17 September	....	....	0.83	1739.5
21 September	....	....	0.82	1630.5
Mean ratio	1.23	....	0.982	....
Standard deviation	0.6146	....	0.2088	....

Reproductive Activities

Before the peak of adults (August 26) had been reached some of the females showed indications of eggs developing in their oviducts. Therefore, a period of 16 days or possibly less was required for their sexual maturation. However, none of the females were carrying spermatophores until September 10. Since the first adults appeared on August 10 and spermatophores were first noted to be attached to the females on September 10, it is certain that males require more than 16 days for sexual maturation.

Following September 10 the intensity of sexual activity was determined by computing the percentage of females that had attached spermatophores. This percentage increased sharply between the 10th and 17th, reached an apparent peak sometime late in September, and then decreased slowly until October 27; thus, sexual activity occurred over a known period of a month

TABLE V. Females of *Limnocalanus johanseni* bearing spermatophores expressed as percent of total females

Date (1952)	Percent
10 September	0
14 September	4.1
17 September	53.8
21 September	44.6
10 October	47.8
17 October	37.5
27 October	34.5

and a half. The data showing this time sequence are presented in Table V.

Egg Hatching

Limnocalanus johanseni does not produce eggs in a sac as do diaptomids. Consequently, eggs must be produced individually or in chains that drop to the lake bottom. Since there were no eggs in any of the samples it is not possible to evaluate egg production in this copepod population. After the eggs were produced they probably remained on the bottom until conditions were favorable for hatching. Some data were taken on the conditions prevailing prior to the time eggs had hatched in the spring of 1952 as well as in the fall of 1952 when eggs were produced in order to determine any causal relations between environmental events and the process of egg hatching.

In an arctic lake temperature would be one of the first factors to be examined in this respect. The temperature conditions prevailing in the spring of 1952 (Fig. 3) before the population presently being studied had hatched were available from thermistor cables operated by the U. S. Geological Survey. These data show that through the winter of 1951-1952 there was a relatively large amount of water beneath the ice. This water comprised approximately 29% of the lake volume at the time when ice development was at its maximum (1 June 52). Its temperature ranged from 0°C where it contacted the ice to 1°C at the mud surface. The geothermal profiles show that below the mud surface there was a reservoir of heat. The temperatures within the mud continually increased, thus providing a reserve of heat which apparently was important in maintaining a stable environment with respect to temperature. It is certain that these eggs were not frozen, and it is possible that the eggs are never frozen in lakes of this region, assuming that there is always a layer of free water at the bottom, because they would be deposited on the surface of the mud where the temperature of the free water is highest.

Between June 1 and July 22 the lake slowly warmed to the point where the ice melted. By July 28 all eggs that were going to hatch had done so, but it is probable that the greater number of eggs had hatched before July 10. Figure 1 shows a small temperature peak before the 15th. These are the temperatures that prevailed in the open areas around the large mass of ice that existed in the center of the lake. Since heat must penetrate the lake from the surface and the surface temperature increased to 2°C at this time, the bottom temperature may have increased above its winter minimum of 1°C to as much as 2°C. The eggs at the bottom of these areas could have been slightly

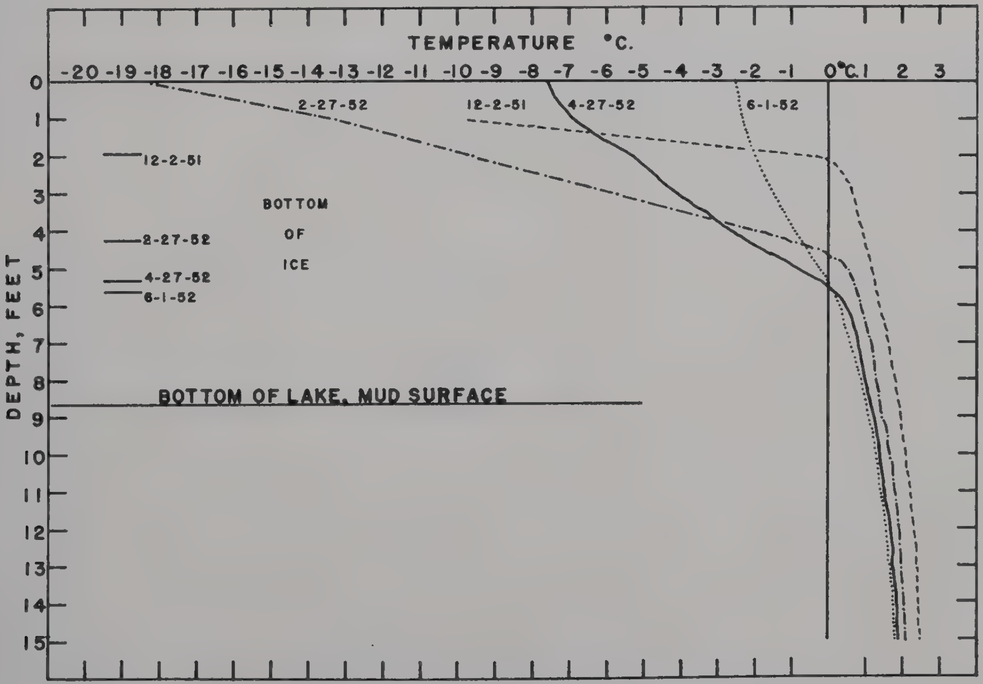

FIG. 3. Geothermal profiles for Imikpuk: U.S.G.S. Official files.

warmed above the minimum winter temperature of June 1. The drop in temperature that followed this occurred when the large mass of ice was melting rapidly, but by this time the bulk of eggs had hatched. This would indicate that temperature may be the causal factor that brought about hatching.

After September 21, 1952, the water temperature was less than one degree above freezing. The first freeze-over occurred on September 25, and by December 1 the ice was 27 inches thick. Through this time the water temperature just under the ice was 0°C, and just above the bottom it did not vary much from 1.8°C. This population was not studied beyond December 1, 1952. By comparison with conditions during the winter 1951-1952, conditions were very much the same. Ice development was approximately equal at this time for both winters.

Environmental factors other than temperature could also influence the hatching process. It is known that the water under the ice had a color of about 75 U.S.G.S. units in the early summer months, as compared to the usual ice-free water color of 25. Also prior to being ice-free the water was relatively high in carbon dioxide (Prescott 1952) and as a consequence was acid. This acidity decreased from a pH of less than 6.0 to 7.4 as the ice melted. There is also the possibility that radiation has a direct effect on hatching. That the hatching is initiated by more than one factor should also be considered.

Length Measurements and Growth Factors

Size measurements are listed in Table VI which are median lengths, with the means of the median lengths for each stage at the bottom of the table.

These length measurements showed that the median size of all stages that appeared after July 25 declined with time (Fig. 4); that is, the first copepodids produced were larger than the later ones in any one stage. For the earlier nauplii (N I, II, III, IV, and V) the length measurements were erratic between the 15th and the 25th. The nauplii in stage VI showed no total change in length from the first to the last day of their existence. Copepodids of stage I showed a slight and probably insignificant decrease during the same period. The median size of stage II copepodids decreased markedly and the medians of the meas-

TABLE VI. Median lengths (mm) of *Limnocalanus johanseni*

1952	N I	N II	N III	N IV	N V	N VI	C I	C II	C III	C IV	C V (male)	C V (female)	C VI (male)	C VI (female)
10 July	0.226	0.301	0.358	0.450	0.571	.....	.....	....	....	....	....	....	....	....
12 July	0.226	0.298	0.375	0.436	0.561	.....	.....	....	....	....	....	....	....	....
14 July	0.226	.....	.....	.....	.....	0.736	.....	....	....	....	....	....	....	....
15 July	.....	0.278	0.375	0.450	0.585	0.750	.....	....	....	....	....	....	....	....
17 July	0.226	0.294	0.352	0.450	0.585	0.736	.....	....	....	....	....	....	....	....
19 July	0.226	0.278	0.389	0.450	0.615	0.726	0.825	....	....	....	....	....	....	....
21 July	0.216	0.294	0.345	.....	0.585	0.750	0.825	....	....	....	....	....	....	....
22 July	.....	.....	.....	.....	.....	0.811	0.825	....	....	....	....	....	....	....
24 July	0.254	0.284	0.358	.....	0.524	0.825	0.831	....	....	....	....	....	....	....
26 July	.....	.....	.....	0.375	.....	0.764	0.825	1.05	1.27	....	....	....	....	....
28 July	.....	.....	.....	.....	.....	.....	0.841	1.09	1.24	....	....	....	....	....
31 July	.....	.....	0.358	0.426	.....	.....	.....	....	1.32	1.52	....	....	....	....
4 August	.....	.....	.....	.....	.....	0.726	0.778	0.913	1.15	1.45	1.72	1.86	....	....
8 August	.....	.....	.....	.....	.....	.....	.....	0.913	1.08	1.30	1.62	1.62	....	....
11 August	.....	.....	.....	.....	.....	.....	.....	....	....	1.17	1.47	1.52	1.93	2.06
13 August	.....	.....	.....	.....	.....	.....	.....	....	....	1.12	1.42	1.44	1.81	2.03
15 August	.....	.....	.....	.....	.....	.....	.....	....	....	1.18	1.40	1.40	1.71	1.82
20 August	.....	.....	.....	.....	.....	.....	.....	....	....	....	1.28	1.35	1.76	1.74
23 August	.....	.....	.....	.....	.....	.....	.....	....	....	....	1.32	1.28	1.76	1.82
26 August	.....	.....	.....	.....	.....	.....	.....	....	....	....	1.25	1.25	1.78	1.79
29 August	.....	.....	.....	.....	.....	.....	.....	....	....	....	1.28	1.39	1.76	1.79
2 September	.....	.....	.....	.....	.....	.....	.....	....	....	....	....	....	1.69	1.76
6 September	.....	.....	.....	.....	.....	.....	.....	....	....	....	....	....	1.69	1.76
10 September	.....	.....	.....	.....	.....	.....	.....	....	....	....	....	....	1.72	1.72
14 September	.....	.....	.....	.....	.....	.....	.....	....	....	....	....	....	1.78	1.82
17 September	.....	.....	.....	.....	.....	.....	.....	....	....	....	....	....	1.69	1.79
21 September	.....	.....	.....	.....	.....	.....	.....	....	....	....	....	....	1.72	1.81
1 October	.....	.....	.....	.....	.....	.....	.....	....	....	....	....	....	1.76	....
10 October	.....	.....	.....	.....	.....	.....	.....	....	....	....	....	....	1.76	1.79
17 October	.....	.....	.....	.....	.....	.....	.....	....	....	....	....	....	1.69	1.79
27 October	.....	.....	.....	.....	.....	.....	.....	....	....	....	....	....	1.72	1.76
1 December	.....	.....	.....	.....	.....	.....	.....	....	....	....	....	....	1.66	1.39
Mean	0.229	0.290	0.364	0.434	0.575	0.759	0.821	0.990	1.21	1.29	1.42	1.46	1.74	1.79

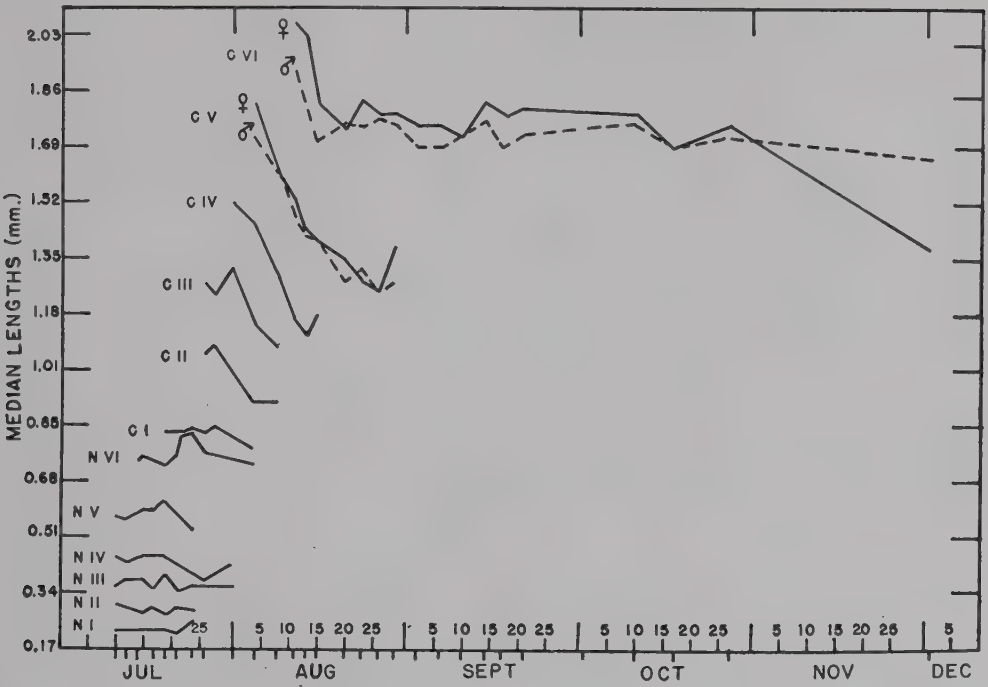

FIG. 4. Median lengths of the instars of *L. johanseni* during the summer of 1952. N = nauplius, C = copepod, C VI = adult. Dates of sampling indicated below the x-axis are: July 10, 12, 14, 15, 17, 19, 21, 22, 24, 26, 28, 31; August 4, 8, 11, 13, 15, 20, 23, 26, 29; September 2, 6, 10, 14, 17, 21; October 1, 10, 17, 27; December 1.

urements of the copepodids that followed showed even more striking decreases. In Table VII are listed the percentage decreases in size for each stage following copepodids of stage I. This decrease expressed as a percentage is calculated as follows:

$$\frac{C_1 - C_2}{C_1} \times 100 = \% \text{ decrease in size.}$$

C_1 is the median length of the earliest appearing copepodids of any particular stage and C_2 is the median length of the last appearing copepodids of the same stage.

After August 15 the adult median size remained more or less constant until October 27 (Fig. 4). The only size measurements available after October are those for December 1, which indicate a relatively great drop in median size. However, these were measurements of only five copepods taken under the ice and it is questionable whether they are representative of the remaining population.

Growth factors[3] for all the stages are listed in Table VIII. These are ratios of the means of the medians listed in Table VI, *i.e.* N II/N I is 0.290/0.299 which is equal to 1.27, the growth factor. These growth factors approximate other similar measurements known for several species of *Diaptomus* (Sewell 1912; Gurney 1931; Comita 1953) and are in conformity with the ratio, 1.26 or 1 : $\sqrt[3]{2}$ for linear growth in all arthropods.

Also presented in Table VIII are surface chlorophyll readings corresponding to the date of maximum numbers for each stage. Surface chlorophyll and growth factors were examined for evidence of causal relationship even though only eleven

TABLE VII. Decrease in size of *Limnocalanus johanseni* by stages. Size measurements are from Table VI

Stage	MEDIAN LENGTH (mm)		Percent decrease in size
	C_1	C_2	
C II	1.05	0.913	13.1
C III	1.27	1.08	15.0
C IV	1.52	1.18	22.4
C V male	1.72	1.28	25.6
C V female	1.86	1.39	25.3
C VI male	1.93	1.66	14.0
C VI female	2.06	1.39	32.5

---

[3] In the study of copepods the term "growth factor" has long been used to denote the ratio of lengths between two succeeding instars (Gurney 1931); for this reason it should not be confused with the same term used in vitamin research.

TABLE VIII. Growth factors of *Limnocalanus johanseni* and surface chlorophyll, Imikpuk 1952

Date (1952)	Stages	Growth factor	Surface chlorophyll (Klett Units)
8 July	N II/N I	1.27	12.0
10 July	N III/N II	1.26	12.5
16 July	N VI/N III	1.19	10.5
18 July	N V/N IV	1.33	9.0
21-22 July	N VI/N V	1.32	8.5
26-27 July	C I/N VI	1.08	8.0
30 July	C II/C I	1.20	6.5
2 August	C III/C II	1.22	4.0
5 August	C IV/C III	1.07	4.0
10 August	C V/C IV	1.11	6.0
26 August	C VI/C V	1.23	8.0

pairs of data are available. The correlation coefficient for these is 0.555 which was found to be significantly different from zero at the 10 percent but not at the 5 percent level.

Bimodality

Copepods are known to exist as two size groups in their immature stages as well as during adulthood. The study of the marine copepod *Calanus* has brought this out rather clearly, and it has been noted in several freshwater species of *Diaptomus*. The existence of two sizes has been observed by several investigators (Gurney 1931), and the larger has been referred to by some authors as a "high form" in contrast to the normal animal which was called a "low form." This phenomenon is probably much more common than is indicated in the literature on copepods.

During the course of this study the measurements of the adults of *Limnocalanus* indicated that bimodality occurred in this population (Fig. 5). When these measurements were plotted on arithmetic probability paper (Figs. 6, 7) the points fall on a sigmoid curve as described by Harding (1949). This treatment shows clearly that this population was bimodal with respect to size. The measurements taken were from the metasome only.

Very early in the adult stage, on August 11, there appeared the first indication that the population was composed of two size groups. On every date following the 11th two size groups were apparent, more or less according to the number of adults measured. This bimodality occurred in both sexes (Table IX). The males occurred as two size groups, the larger of which varied from 1.11 to 1.19 times the smaller. For the two sizes of females the larger varied from 1.11 to 1.23 times the smaller. There was no perceptible change in the mode of the size for the two groups of males and the two groups of females from the time the adults appeared until October 27, the last date on which reliable measurements could be obtained.

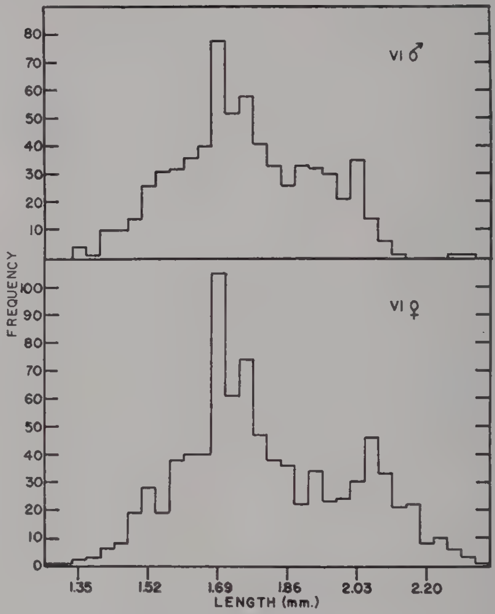

FIG. 5. Length frequency histograms for all the adult males and females of *L. johanseni* showing the bimodality of the two groups.

TABLE IX. Bimodality of the adult males and females

	Males		Females	
Median length (mm)	1.69	1.96	1.69	2.06
Standard deviation (mm)	0.14	0.066	0.13	0.11
Percentage composition of total males & females	74	26	69	31

A possible explanation of the existence of bimodality as shown by the above measurements is as follows. After copepodids of stages II and III the first copepodids to appear in each instar were the largest (Fig. 4). Since each instar is larger than the preceding one and no doubt possesses mouth parts that are better able to retain food, as well as being able to filter more water because of their size, those appearing first in each stage could have a trophic advantage over those not yet molted. This could result in a larger size for those molting before the food supply diminished to a point where it was limiting. According to the data of Prescott (1952), just after the ice melted about July 22, the algal cell counts showed a relatively sharp drop. This decrease in the food supply could have produced the growth differential apparent as bimodality in the adult population.

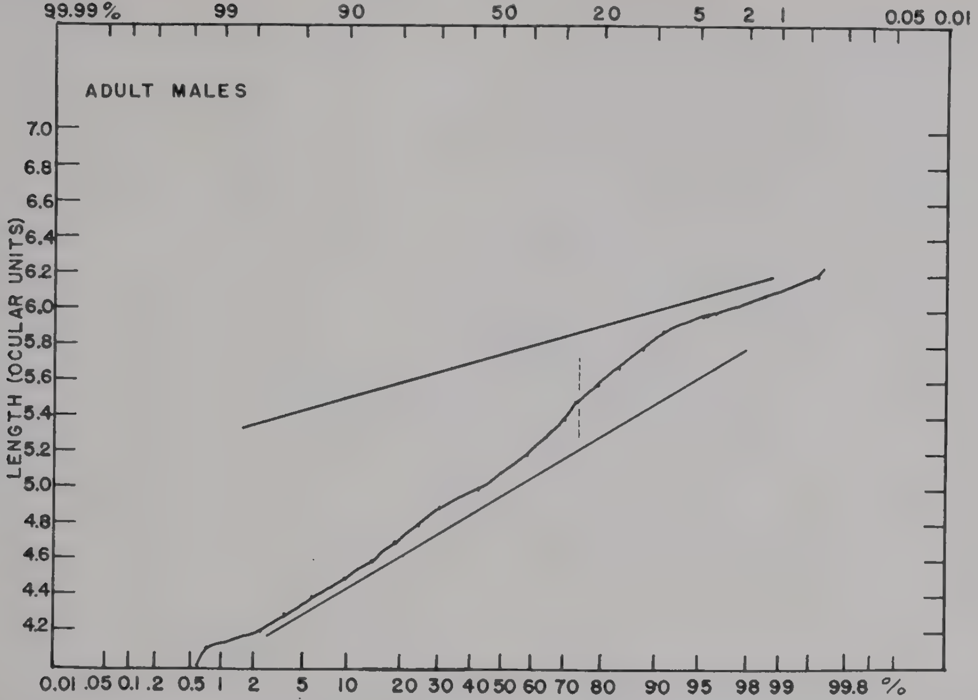

FIG. 6. Analysis of the size distribution of adult males on arithmetic probability paper using data of all males measured. The point of inflection separates the two populations; the larger size is to be found to the right of the point of inflection, the smaller to the left of the point, which is indicated by the light dashed vertical line. One ocular unit = 0.338 millimeters. (See Table IX).

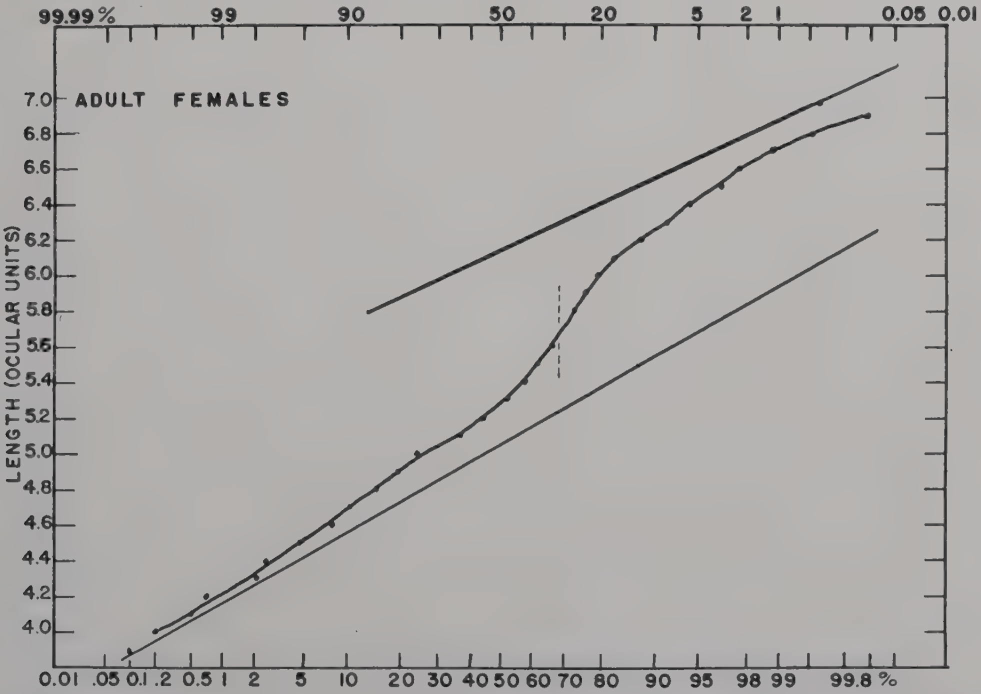

FIGURE 7. Analysis of the size distribution of adult females on arithmetic probability paper using data of all females measured. The point of inflection separates the two populations, the larger size is to be found to the right of the point of inflection, the smaller to the left of the point, which is indicated by the light dashed line. One ocular unit = 0.338 millimeters. (See Table IX).

Phytoplankton-Zooplankton Relationships

There are many studies in the literature showing that in marine waters phytoplankton increases and maxima of zooplankters coincide. Clarke (1939) pointed out some of the more striking examples that show this. In the Clyde Sea area the work of Marshall, Nicholls, and Orr (1934), in the North Sea the work of Wimpenny (1936), and in the English Channel off Plymouth the study of the seasonal succession of events by Harvey, Cooper, Lebour, and Russell (1953), provide convincing evidence of the existence of a phytoplankton-zooplankton relationship in those waters.

In fresh waters this kind of evidence has been lacking, but the data show somewhat more indirectly that this relationship exists. There is little doubt that this relationship is based upon the grazing of phytoplankton by zooplankton, but there is still a scarcity of adequate data to support it. The very recent work of Anderson, Comita and Engstrom-Heg (1955) does support it, and the data taken in this study offer further evidence in this direction.

A study of the data presented here on *Limnocalanus* suggests that a food scarcity existed, and that this was due to grazing. The evidence presented in support of this is that which concerns the *Limnocalanus* population alone, but data on the total numbers of *Daphnia* were also available and these lend further support in this discussion. This evidence is found in several sets of data: the chlorophyll-extracts curve, the algal-cell counts (Prescott 1952), photosynthesis, and the length measurements.

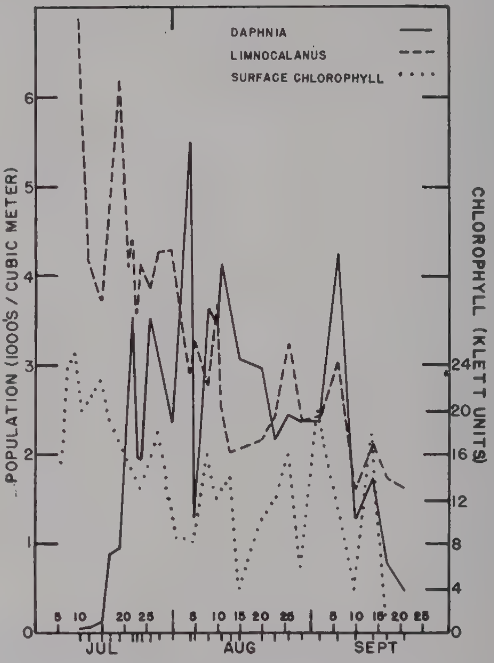

FIG. 8. Total numbers of *Daphnia* and *L. johanseni* during the summer of 1952. Surface chlorophyll is plotted from the acetone extracts.

Prior to July 22 algal extracts and cell counts were at their seasonal maximum. After the 22nd these showed a progressive decline. From July 21 to 30 stage VI nauplius and the next two succeeding copepodids had reached their peak (Fig. 2) and most probably were exerting progressively stronger intraspecific competition for food because of the size increment accompanying each stage. The algal-extracts curve (Fig. 8) shows a minimum at this time, indicating that grazing was seasonally at its heaviest. This is also supported by additional evidence from the study of photosynthesis. Earlier it was mentioned that photosynthesis was studied in the lake during the time the copepod population was undergoing its larval development, which was at the time that the algal data showed a progressive decline by both the extracts and cell counts. The production of photosynthetic oxygen during this period showed a progressive increase (Comita and Edmondson 1953). This would mean that the planktonic grazers present were being fed better than at any other time during the summer; yet this was not adequate for complete survival of the various instars as shown by the continued decrease in the total population (Fig. 9 and Table X). Also this resulted possibly in the size bimodality of the surviving adults previously described.

It is possible that the over-all low temperatures for the summer restrict the algal population by limiting the rate of growth or division of the algal cells. This may be one of the important factors that limits the food supply, thus by starvation making it impossible for many of the copepod instars to molt into the next stage.

Daphnia was present at the time the copepod nauplii were present (Fig. 8). It is quite likely that *Daphnia* grazed the algae even more heavily than did the larval copepods since the algal population never did return to the peak of the earlier part of the season and the number of *Daphnia* increased until mid-August (Edmondson 1955).

Apparently the algal population was sufficient to sustain the survivors adequately until October 27 in spite of the thickening ice cover, which through November increased to 24 inches. Also during this period daylight hours were fast diminishing, and on November 19 the U. S. Weather Bureau pyrheliometer located at the village of Barrow ceased operation. Thus the photosynthetic part of the basic food crop could not continue to exist, although the heterotrophic organisms could still maintain themselves on suspended organic material as well as bottom organic material. Since no data were taken on the population of protozoa and bacteria under the ice, it is not possible to evaluate their part in the basic food crop.

Mortality Rates

Study of the regression line (Fig. 9) shows that the total population of all stages was about 5000 copepods per cubic meter on July 10, the earliest collecting date. By August 1, the approximate date when copepodid III was at its peak, the population was 3600 per cubic meter. The decreases in the population calculated as percentages as well as mortality rate approximations are shown in Table X.

The regression line of the total population numbers was found to have the equation log $y = 3.45 - 0.00681\,X$. The slope of this line,

$$\frac{dy}{dx} = (-44.793)\ (1.016^{-x}),$$

constitutes an approximate daily rate of mortality. The regression line is extrapolated beyond September 21 because quantitative sampling stopped on that date. The upper and lower confidence limits at the five percent level of significance are also shown in Figure 9.

TABLE X. Percentage decreases and mortality rate approximations of *Limnocalanus johanseni*

Date (1952)	Population all stages per m^3	Cumulative % decrease	% decrease from previous date	Approximation of daily mortality rate*
10 July	5000	..	..	80.2
1 August	3600	28	28	56.7
1 September	2240	55	38	34.9
1 October	1400†	72	38	22.1

*10 July is first day of sampling.
†Extrapolation.

Mortality in the adult population was heavy before the lake began to freeze. Their numbers dropped from a peak of 3150 per cubic meter on August 26 to 1631 on September 21, a decrease of 51.63 percent.

By the first of October, 72 percent of the original population had died out. Since five copepods were taken on the date of the final collection, 1 December 1952, it is possible to state that the population did not die out before that date. Through the winter no more collections were made. However, a collection from two widely separated holes cut in the ice made on April 23, 1953 showed no copepods whatsoever, neither larvae nor adults. Also at the time of the first collections in July, 1952, there were no adults in any of the samples. This evidence and the lack of photosynthetic food indicates that this copepod population died out during the latter part of the winter and the wintering-over occurred in the egg stage.

Length-weight Measurements and the Ponderal Index

Growth data on copepods in the literature are

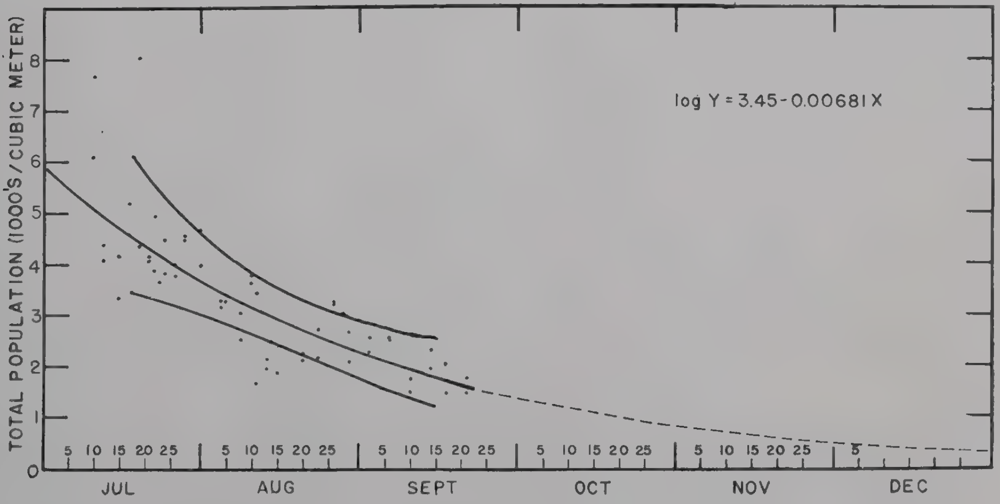

FIG. 9. Regression curve showing the mortality of the *L. johanseni* population with upper and lower confidence limits indicated. Each dot represents the total number of *L. johanseni* (all stages) counted in one sample, two samples having been counted for each date.

TABLE XI. Length, weight, and ponderal index data for *Limnocalanus johanseni*

Stage	Mean length (mm)	Number weighed	Wet weight (mg)	Dry weight (mg)	% water	Dry weight per individual (mg x 10^3)	Ponderal index ($K=W/L^3$)
N VI	0.778	105	3.0	0.3	90.0	2.86	6.07
C I	0.791	100	3.7	0.4	89.2	4.00	8.08
C II	1.028	101	8.9	0.9	89.9	8.91	8.20
C III	1.158	55	6.0	0.6	90.0	10.91	7.03
C IV	1.361	87	21.5	1.7	92.09	19.54	7.75
C V (male)	1.498	60	21.2	1.9	91.98	31.67	9.42
C V (female)	1.519	70	23.4	2.3	90.17	32.86	9.38
C V (mean	1.509	..	....	...	.....	32.16	9.36
C VI (male)	1.732	61	35.9	2.7	92.48	44.26	8.52
C VI (female)	1.757	60	36.0	2.7	92.50	45.00	8.30
C VI (mean)	1.745	..	....	...	.....	44.63	8.40

very scarce. The following data (Table XI) are offered with the qualification that they were taken on specimens after two years of preservation; nonetheless, they appear to be in the right order of magnitude. Even though it is likely that the data are valid only when used for comparing the stages in this study, it is felt that their presentation is justified.

The relationship W/L^3, called the ponderal index, was computed from these data to note any progressive change in proportion of weight to length. In copepodid V the ponderal indices, 9.38 and 9.42, are greatest. It is in copepodid V that sufficient sexual dimorphism occurs so that the sexes can be clearly recognized, and this may possibly account for the increase in ponderal index in this stage. Also there is a relatively great morphological change in the molt from N VI to C I. This is accompanied by a considerable change in ponderal index between these two instars.

When the log weight and the length are plotted (Fig. 10), the points fit a straight line very well. For this curve the mean lengths used were those of the specimens weighed. The equation for the curve was found to be log $W = 1.19\,L - 0.346$, and the slope of this regression line was found to be significantly different from zero at the one per-cent level.

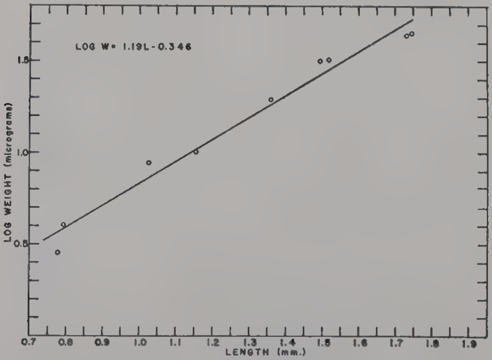

FIG. 10. Regression line of log weight on length for the following stages (preserved) of *L. johanseni*: N VI, C I, C II, C III, C IV, C V, and C VI (adults).

The water content of these preserved specimens is much greater than that found for *Diaptomus sicilis* in Lake Lenore in Washington by Comita (1953). Also the weight is considerably greater for *D. sicilis* of Lake Lenore. This difference may be due to the fact that the Lenore *sicilis* specimens were weighed immediately after the animals had died without use of preservative.

Comparison with Other Calanoid Life Cycles

The work of Comita (1953) in several Washington lakes and that of Ravera (1954) in Lake Maggiore indicate that for those few planktonic calanoids whose life cycles are known as many as three generations were noted in one year, and depending on the limnological conditions, one, two, or three generations have been produced. Ravera's work showed that *Mixodiaptomus laciniatus* was monocyclic and that its life cycle required the entire year. The life cycle of *M. laciniatus* was very much like that of *Diaptomus ashlandi* in Lake Washington in that *D. ashlandi* also required the entire year for development from egg to adult. In addition these two calanoids are similar in that they produce eggs at the year's end and the nauplii must develop during times of cold water temperatures.

Limnocalanus johanseni also produced eggs in the fall, but in the Arctic these must await a much greater passage of time before development can take place. Its entire life cycle is greatly accelerated compared to that of *D. ashlandi* and *M. laciniatus,* being somewhat more comparable to one generation of the life cycles of *Eudiaptomus vulgaris,* studied by Ravera, and *D. sicilis,* studied by Comita. But even in these latter the development is considerably slower, requiring several months.

Gurney (1931) outlined the life cycle of *L. macrurus* in Sweden. Apparently *L. macrurus* has a life cycle very similar to that of *L. johanseni*. Of particular note is that resting eggs are produced and that these sink to the bottom and hatch out in March and April, the adults of the preceding year dying out in the spring. He stated that development from young to full grown copepods required about two months and that reproduction could not occur until after the gonads matured, which was sometime during October or November when the water temperature had dropped to about 7°C. As in *L. johanseni* in a single year there was one generation only and the individuals lived for less than one year.

Gurney (1931) further stated that due to the presence of a modified third segment in the 5th leg of the male, *L. johanseni* must be considered to be more nearly related to *Centropages* than are the other species of this genus (*Limnocalanus*). Of particular interest is the fact that *Centropages hamatus* is an estuarine form and was found by Derzugin (1925) in a "relict" lake in the island of Kildin on the Murmansk Coast. Other estuarine records for this species are abundant.

Records of *L. johanseni* are scarce. However, Imikpuk is situated on the arctic coast of Alaska only a few hundred yards from the Arctic Ocean and is physically connected to the Arctic Ocean by a very shallow marsh which separates it from a lagoon that is continuous with the Arctic Ocean. The water in Imikpuk was nonetheless fresh; salinities were measured several times and these were very low, being of the magnitude of ordinary fresh waters (about 35 ppm NaCl). The physical connection does, however, provide the avenue for invasion of marine forms, or rather provides evidence that Imikpuk is a recent separation.

Of further interest is the fact that although more remote morphologically, *Calanus finmarchicus* has a life cycle in which the time required for one generation is comparable to that of *L. johanseni*.

Another very interesting question now poses itself. What is the life cycle of *L. grimaldii?* In view of the morphological similarities between *grimaldii* and *johanseni,* are their life cycles similar developmentally and morphologically? Because of the close proximity of Imikpuk to the Arctic Ocean and the existence of *grimaldii* in those coastal waters (Wiley 1920), the data offered in this paper are of importance in deciding any relationship that may exist between these two species.

SUMMARY

The life cycle of an arctic calanoid copepod, *Limnocalanus johanseni* Marsh, was studied in samples taken from a small shallow lake called Imikpuk, located at Point Barrow, Alaska, during the summer months of 1952 from the time the lake ice melted until the lake froze over again.

Other animals found in this lake were *Cyclops scutifer* Sars, *Eurytemora canadensis* Marsh, *Daphnia pulex* var. *tenebrosa* Sars, two species of Anostraca, one notostracan, *Apus,* and two other calanoids, *Diaptomus glacialis* Sars and *Diaptomus alaskaensis* M. S. Wilson. Rotifers of the genera *Kellicottia, Synchaeta, Notholca,* and *Keratella* were found to be abundant in the samples. As far as is known there were no fish in Imikpuk.

Imikpuk is a freshwater lake separated from the Arctic Ocean by a shallow marsh. Its temperature cycle in 1952 was as follows: the winter ice melted about July 22 and the lake temperature reached a maximum of 10.5°C by August 10, then rapidly dropped to freezing again by September 27. The lake was free of ice for a period of 65 days in 1952.

The plankton of Imikpuk was studied by taking quantitative hauls at time intervals that varied from one to five days. Two consecutive hauls were made on each date. A Clarke-Bumpus plankton sampler was used for making all hauls. The constant, liters per revolution, for this particular instrument was found to be 4.6.

When the plankton was counted the population deviation from the mean for the two samples taken on each date was computed. Expressed as a percentage this was found to average 8.54 percent of the mean for all samples and it ranged from 0.158 to 35.3 percent.

The instar populations were determined by counting and identifying the stages. Each of the stages was recognized by the appearance and state of development of the appendages as well as the body form.

Hatching of the eggs occurred during the time the ice was melting. All six nauplius stages were found in the first samples taken. The life cycle was found to consist of six nauplius and six copepodid stages in addition to the egg.

The duration of each instar was obtained by estimation of the time interval between peaks of each stage. These time intervals in days were estimated for all stages as follows: for nauplius stages I, II, and III, less than four days; for nauplius IV, 2 days; N V, 2.5; N VI, 5; for copepodid I, 3.5; C II, 3; C III, 3; C IV, 5; C V,

16; C VI (adult), approximately 120 days.

Data taken on the reproductive activities indicated that 16 days or possibly less were required for sexual maturation in the adult females. Based upon the time of appearance of spermatophores on the females it is certain that males required more than 16 days for sexual maturation. Sexual reproduction occurred over a period known to be at least 47 days after September 10.

Some observations were made of environmental conditions existing while egg hatching occurred in the spring and after egg production in the fall. These observations indicate that a slight increase in temperature may have initiated egg hatching. Other possible stimuli for hatching are also discussed.

Median lengths for all stages in the samples are presented. The means of these were found to be as follows (mm): N I, 0.229; N II, 0.290; N III, 0.364; N IV, 0.434; NV, 0.575; N VI, 0.759; C I, 0.821; C II, 0.990; C III, 1.21; C IV, 1.29; C V (male), 1.42; C V (female), 1.46; C VI (male), 1.74; C VI (female), 1.79.

The ratios of lengths of succeeding stages is called a growth factor. Growth factors for all stages are computed and found to approximate $\sqrt[3]{2}$ in conformity with Dyar's law for arthropod size increment in succeeding instars. The correlation coefficient for growth factors and chlorophyll extracts was found to be 0.555 which was significantly different from zero at the 10 percent level. Acetone extracts of chlorophyll were used as a measure of food supply.

When the length measurements were examined by plotting them on arithmetic probability paper, bimodality with respect to size in the adults was noted. Of the entire male adult population 74 percent had a median length of 1.69 mm while the other 26 percent had a median length of 1.96 mm. In the adult females 69 percent had a median length of 1.69 mm while the other 31 percent had a median length of 2.06 mm.

A possible explanation for this bimodality is advanced. This explanation is based upon the possibility that those larval stages appearing first in any instar would have a trophic advantage over those appearing later in the same instar. This could result in a larger size for those molting before the food supply was diminished to a point where it was limiting.

Data suggesting that grazing of zooplankters was responsible for depletion of the food supply are presented.

A mortality curve for the total population is presented. The regression line of the population numbers was found to have the equation: $\log y = 3.45 - 0.00681\,x$. The slope of this line is presented as an approximation to the daily mortality rate of this population. The extrapolation of this curve indicates that this adult population died out sometime after the first of the following year (1953). A collection during the winter of 1953 showed no copepods whatever, neither larvae nor adults. This further indicates that the population winters over in the egg stage.

Weight data were taken on nauplius stage VI and all the copepodids. A regression line of log weight on length was calculated. The equation of this line was found to be $\log W = 1.19\,L - 0.346$. The ponderal index was also computed from these data, and this index was found to be largest for copepodid stage V, the stage in which sexual dimorphism is first apparent.

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NOTES AND COMMENT

ORIGIN OF SOUTHERN APPALACHIAN GRASS BALDS

Whittaker (1956) in his recent monograph on the "Vegetation of the Great Smoky Mountains" recognizes four high altitude "discontinuous" communities-spruce fir forest, beech gaps, heath and grass balds, and all as having originated under the impact of natural environmental factors.

This note is to show that the grass balds are exceptional and cannot possibly have originated under the natural condition of "extreme exposure" as suggested by Whittaker for the following reasons:

1. The original grass balds are few in number, of restricted size and are widely distributed along the high ridges. Views from high summits which take in dozens of miles of distant ridges, may not disclose a single grass bald. Literally hundreds of miles of ridges above 6000 feet are completely devoid of these small openings in the forest dominated by the mountain oatgrass. That along these irregular ridge tops, "extreme exposure" only occurs at intervals of ten, twenty or fifty miles, is of course inconceivable. If "extreme exposure" initiated and maintained the grass balds, most of the high altitude ridge tops of the southern Appalachian mountains would be in grass.

2. Whittaker correctly states "The change from forest to grass bald is abrupt." But he fails to explain how "extreme exposure" may operate in an equally abrupt fashion. Though he includes the balds under "topographic climaxes" by which he indicates the exposure is due to local ridge site, he fails to give evidence from any bald that the site conditions or the local climate changes so abruptly as to result in the sharp contrast of mature forest in immediate contact with lush stand of oatgrass. Natural ecotones, especially of the exposure type could never be confined to a few feet in width as are these bounding the grass balds. Climatic ecotones are universally gradational and broad.

3. On many forested ridge tops, the old, well-defined Indian trails are covered by almost exactly the same oatgrass-dominated herb complex as are the balds. Protected by the forest on each side, these sites cannot be ones of "extreme exposure," yet for long distances the trail community is identical with the grass bald ones.

The three points made above, not only disprove any "natural" explanation of grass bald origin, but indicate them to be artifacts or archeological disclimaxes. The original grass balds, first seen by white men, are naught but expanded trails, camp sites of the early hunter Indian who preceded the lowland Cherokee farmer of Bartram's day. Fifteen out of twenty-two balds the writer has visited were on gentle, warm, south-facing slopes, just above or near to springs. This correlation with high mountain springs is most significant in light of the fact of the extreme paucity of such springs. For a fuller discussion of the Indian theory of origin, see the writer's paper (Wells 1937).

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EFFICIENCIES, SIZE OF ORGANISMS, AND COMMUNITY STRUCTURE[1]

In the following paragraphs are presented some unproven ideas and concepts about communities and their adjustment in natural circumstances. Although it is presumed that there will be many exceptions, these concepts are proposed tentatively as generalizations. It should be emphasized that where the types of behavior discussed here are meant to apply to whole communities, they do not necessarily refer to the functions of single organisms.

Hump-shaped Relationship of Production and Efficiency With Varying Light Intensity

In Figure 1, the production rates of natural plankton communities in a lake obtained by Manning, Juday, and Wolf (1938) at several levels are plotted as a function of efficiency of photosynthesis. Also indicated are the properties of production and efficiency obtained in much of the work that was done on the quantum requirements of algal cultures where low light intensities were used. The curve is hump-shaped. As discussed below, it may be suggested that a hump-shaped relationship of production and efficiency is general when only the light intensity is varied. At low light intensities, in spite of high efficiencies the energy flow is so small that the production is small. At high light intensities the production is greater in spite of lowered efficiency.

That no natural community, agricultural plot, or experimental situation resembling nature has apparently achieved high efficiences above 10% under full daylight intensities may be interpreted as an evidence for the inverse relationship of efficiency and production that occurs on the right-hand portion of the hump-shaped curve. (See data in Rabinowitch 1951). Another example was the effort made to achieve high efficiencies under natural light conditions in culture efforts (Burlew, *et al.* 1953) which was not successful.

Optimal Efficiency-Maximum Power Hypothesis Applied to Primary Production

If curves like that in Figure 1 are typical, there is a maximum production associated with the peak of the curve and an associated relatively low efficiency that is optimum. If the primary production of communities is important for their competitive survival (Lotka's principle), there will be a tendency for communities to

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[1] Comment presented in a symposium, Primary Production in Waters, Sept. 6, 1955, at the Ecological Society of America Meeting, East Lansing, Michigan. Appreciation is expressed to E. P. Odum, John Teal, W. T. Edmondson, and Jacob Verduin for suggestions.

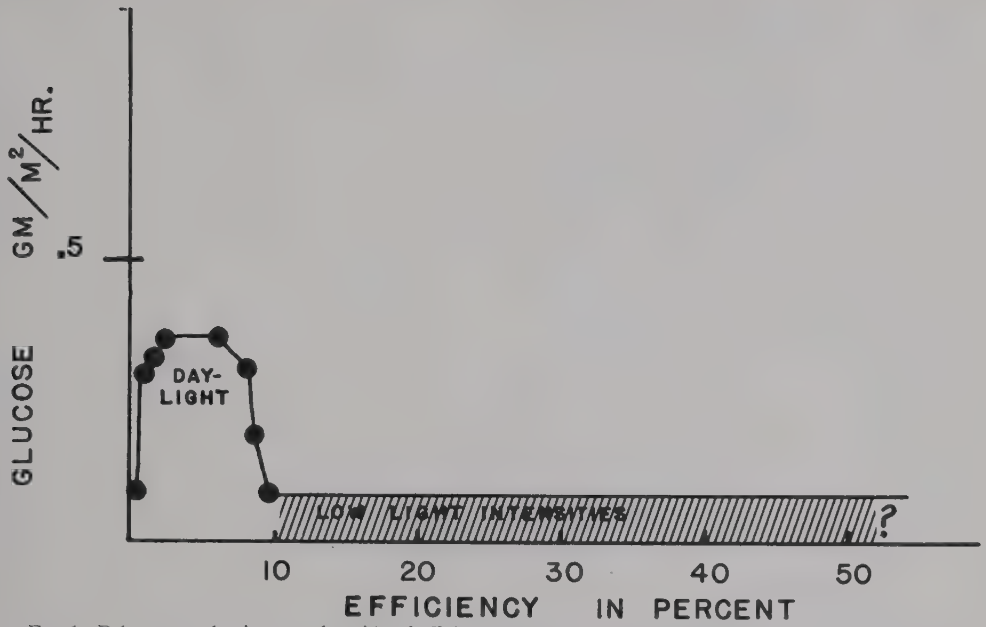

FIG. 1. Primary production as a function of efficiency showing a low optimum efficiency for maximum power output and a low power output with maximum efficiency. The plotted points are from bottle experiments in lake water by Manning, Juday, and Wolf (1938). Values for high efficiencies but low production are summarized in Rabinowitch (1951).

be adjusted to that production and efficiency corresponding to the peak of the hump-shaped curve. There is thus a reason to expect somewhat similar low efficiencies among many successful naturally-adapted communities, although the exact position of the peak may be a function of nutrient and carbon dioxide levels.

In accounting for the hump-shaped curve of production and efficiency, we turn to the basic nature of energy transfer as expressed in the second law of the thermodynamics. In a theoretical derivation given elsewhere (Odum and Pinkerton 1955), it was demonstrated that for simple physical systems under certain proscribed conditions, the second law of thermodynamics required a hump-shaped curve of power and efficiency. Although there is apparently no question of the validity of the principle for simple physical systems, the application to more complex biological systems like community photosynthesis is hypothetical. However, it is proposed that the hump-shaped type curve of Figure 1 is typical, and rooted in the second law of thermodynamics. If the principle is general, attempts to calculate increased world food potentials on the basis of efficiencies obtained in low light experiments should cease.

The Application of the Size-Metabolism Generalization to Photosynthesis

That the metabolism per gram of heterotrophic organisms is inversely related to body size in a somewhat varying $\frac{2}{3}$ power function is a rough generality possibly based on the surface-volume limits to various diffusion processes (Zeuthen 1953, Bertalanffy and Pirozynski 1953). The importance of size effects in determining rates of turnover in zooplankton populations has been discussed by Harvey (1955). Let us now consider size effects in the phytosynthesis of the plants.

In the previous section, a reason was given for expecting naturally adapted, competitive communities to develop similar, moderately low efficiencies when adjusted to similar light regimes. Here efficincy is defined as the per cent of absorbed light of usable wave length that is converted into organic matter. If communities (not individual plants) tend to develop similar photosynthetic efficiencies, there will tend to be similar total photosynthetic power outputs of glucose on an *area of community* basis. This reasoning is based on the tendency for adapted communities to develop sufficient depth of chlorophyll-bearing tisses to absorb most of the available light. The similar efficiency of about 2.5% found for both *Chlorella* cultures and adjacent grass plots (Wassink, *et al.* 1953) is a good illustration of the tendency for similar productive rates to develop in adapted communities.

Suppose the producers do tend to metabolize at the same rate of output per area of community, and suppose size effects hold for photosynthesis as well as for respiration. Then, communities made up of small plants like *Chlorella* growing in steady state should sustain only a small standing crop biomass at any one time in order to achieve the same output per area exposed to the sun as communities with larger plants. Conversely, the big plants in climax rain-forest communities should require a much larger standing crop of photosynthetic biomass to achieve the same production because of the slower metabolism per gram of tissue. Next, we ask if there is any factual basis for the proposed inverse relationship of photosynthesis per gram and individual size in naturally adapted communities.

In Figure 2, aquatic photosynthetic rates on a gram basis under natural light or maximum photosynthetic adjustments are plotted from Verduin (1952) as a function of size. Some aquatic leafy plants are also included

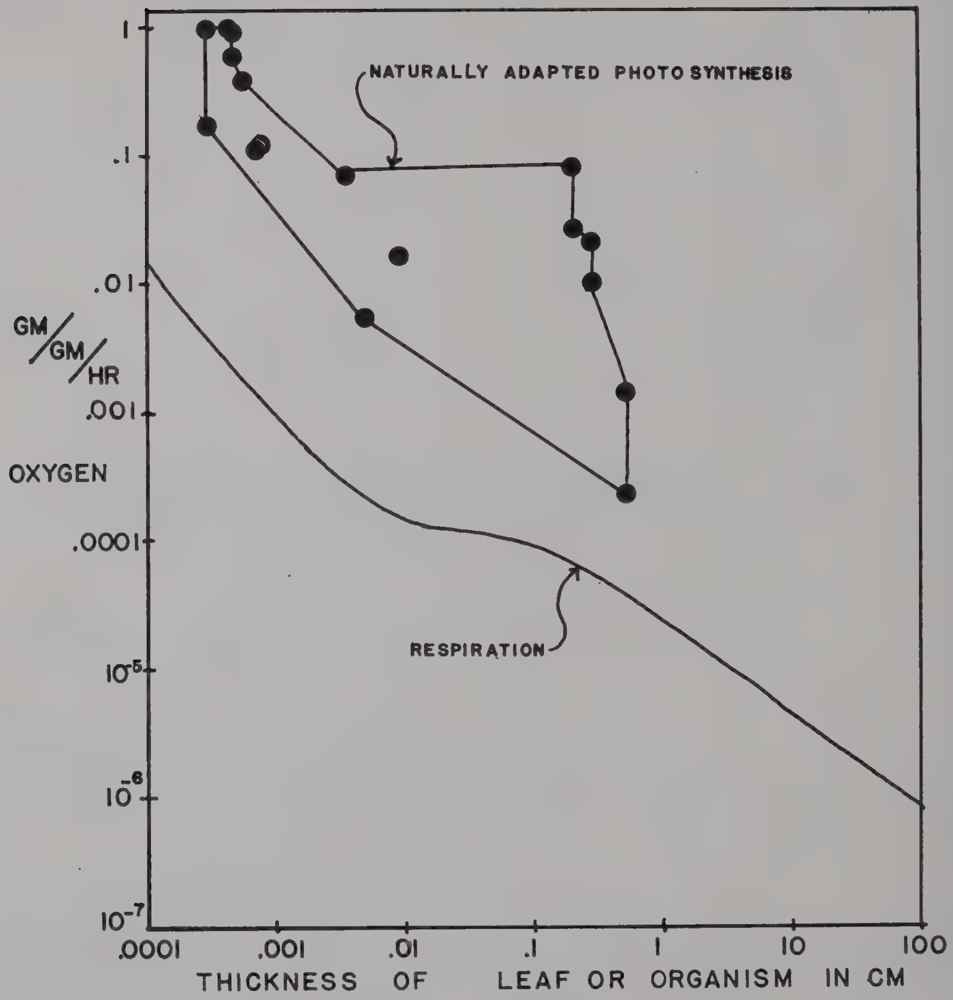

FIG. 2. Metabolism per gram of biomass as a function of organismal size. A line summarizing respiration of heterotrophic organisms was obtained from data in Figure 1 of Zeuthen (1953). The points representing naturally adapted photosynthesis were taken from data collected by Verduin (1952).

with the appropriate leaf thickness being used as size. It is quite apparent from the graph that there is a size effect over a wide range of size just as in respiration processes. The slope is not inconsistent with the slope for animal and bacterial respiration as obtained from Zeuthen (1953). Thus, if one knows the light intensity, the size of the producer, and the rough efficiencies usually found in natural communities, one can compute the potential steady-state biomass (carrying capacity) without direct empirical measurements. At least, one has a basis for obtaining orders of magnitude theoretically without even knowing the species involved. If valid, this could be a useful process of general geography and practical conservation where estimates must be made for large areas where empirical measurements have not been made.

Biomass Pyramid Shapes and Production

Pyramids of biomass are convenient graphic ways of representing the standing crop (stock) of communities according to their trophic levels, but a general statement has not been made to indicate the kinds of pyramids that are possible in different situations. Whereas some environments have more producer biomass than consumer biomass (Odum 1953, Odum and Odum 1953 and 1955), in other communities, such as in planktonic communities, the pattern may be reversed. Some of the concepts given in the preceding paragraphs are included below in an attempt to summarize the relationship of pyramid structure and production rates under steady state conditions.

Three principal mechanisms are important in regulating the expression of production in the standing crop. One is the ratio of the animal consumers to the bacterial consumers. The second is the distribution of organismal size relative to the trophic levels. The third is the relative quantitative dominance of gross primary production (P) and community respiration (R) as represented by the P/R ratio.

To illustrate the working of each effect separately from the others, some pyramids of biomass have been calculated in Figure 3. In Figure 3c, the effect of increasing organismal size up the food chain is compared with decreasing organismal size up the food chain. In this example, half of the primary production has been assigned to bacteria, which due to their small size and hypothetically large metabolism are for practical purposes invisible components. Metabolic values for the bacteria were taken from the respiration line in Figure 2. In these two pyramids, a P/R of 1 implying no net imports or exports was assumed.

In Figure 3b is shown the effect of different ratios of decomposers (bacteria) to other consumers. A constant organismal size for all non-decomposer trophic levels and a P/R of 1 are assumed for this example. It is clear that the larger the bacterial component, the smaller is the mass of consumers supported since the bacteria tend to be negligible as standing crop biomass.

In Figure 3a are shown pyramids illustrating the effect of different quantities of imports and exports. A case is shown with large imports ($P/R < 1$), one with self-sufficiency ($P/R = 1$) as in two previously discussed groups of pyramids, and one with a net export ($P/R > 1$). Here, bacteria have been assumed to get half of the primary production, and size has been assumed to be the same for all trophic levels. Here the higher P/R ratios give the lower biomass in the consumer trophic levels. A community which is either exporting or storing organic matter (in excess of its imports) tends to have a small top. Harvestable agriculture, successional communities, and communities building up organic sediments are of such type. Silver Springs is an example of a case where the organic matter is exported downstream. The other extreme is represented by a sewage polluted stream, where the large imports relative to exports can support a considerable biomass that is not based on a photosynthetic energy supply. P/R measurements of stream communities are given elsewhere (Odum 1956).

In most communities, the three effects described above are all in operation. The types of pyramids that result under these interacting circumstances areas are as yet little known. As data become available, calculations like those in Figure 3 will permit one to estimate unknown phases of community metabolism from the standing crop. For example, from production measurements, from the organismal sizes, some idea of the invisible parts of the community, the bacteria, may be computed.

Criticism of Some Definitions of Consumer Productivity

In an imaginative paper, Lindeman (1941) quoted Hutchinson's formulation of the relationship of standing crop (Λn) to energy intake (λn) and energy loss ($\lambda \acute{n}$) for trophic level n as follows:

$$\frac{d\Lambda n}{dt} = \lambda n + \lambda \acute{n} \qquad (1)$$

As seen in the energy flow diagram in Figure 4, there are too many major routes of energy flow through each trophic level for the above scheme to be applied. However, Lindeman applied these concepts to several communities by making the quantity (λn) in the above expression serve as a definition of production. In this procedure, a very misleading and inconsistent usage was begun which if not actually incorrect has created an apparently unrecognized confusion in the definition of production. In the top diagram in Figure 4 Lindeman's usages of symbols of equation (1) above have been added to an energy flow diagram previously used by the present author as a convenient method of clarifying concepts of community energetics (Odum 1956).

The inconsistency in Figure 4a is in the use of the symbol for production in the sense of rate of synthesis of organic matter in the first trophic level while using this symbol in the consumer trophic levels to mean production in the sense of energy intake (consumption, assimilation).

In a series of otherwise clear formulations of production concepts, Clarke (1946, 1954) has used a set of bar diagrams to show the fate of the energy which enters a community as sunlight. Just as was done by Lindeman, Clarke has defined production for the herbivore and carnivore trophic levels as the rate of energy uptake. These usages by Clarke and Lindeman have been widely quoted and included in reference sources such as Allee, *et al.* (1949).

In contrast, the principal idea of production is widely accepted as the rate of synthesis of organic matter whether by plants or animals. To use the term production to mean rate of energy intake is quite contrary to the ordinary English usage as well as its ecological usage by many.

The difficulty in part comes from attempts to divide production processes at a consumer trophic level into gross production and net production just as is done for the primary producer trophic level. In the primary producer trophic level, the gross production is the total result of autotrophic photosynthesis and can be measured by oxygen release. The net production is the organic synthesis remaining after plant respiration has dispersed some of the gross production as heat. In the higher trophic levels however, there is no process comparable to gross production of the primary producers. There is only one measurable production, the net growth and organic synthesis that results from heterotrophic metabolism based on ingested food materials. To assign the term gross production to consumer assimilation (energy intake) is to make production synonymous with total metabolism (respiration plus synthesis). This is no more pertinent than considering the rate of fuel consumption of a bonfire as the production of the bonfire. One possible source for this objectionable viewpoint is the mistaken notion that all of the energy that enters an animal is transformed into new organic matter or equivalent useful work before being expended as heat. Such an assumption is contrary to the second law of thermodynamics.

It is thus suggested that consumer production be defined as rate of new organic synthesis rather than as rate of consumption. In Figure 4b are given a set of symbols in a more consistent usage with I_n for the energy intake, R_n for respiration and P_n for the new organic synthesis (net production) for trophic level n. P is the gross primary production. In this usage, there is no gross production beyond the producer trophic level. Since the primary production trophic level differs from the consumer trophic levels by having a double energy transfer, concepts and symbols must indicate this difference.

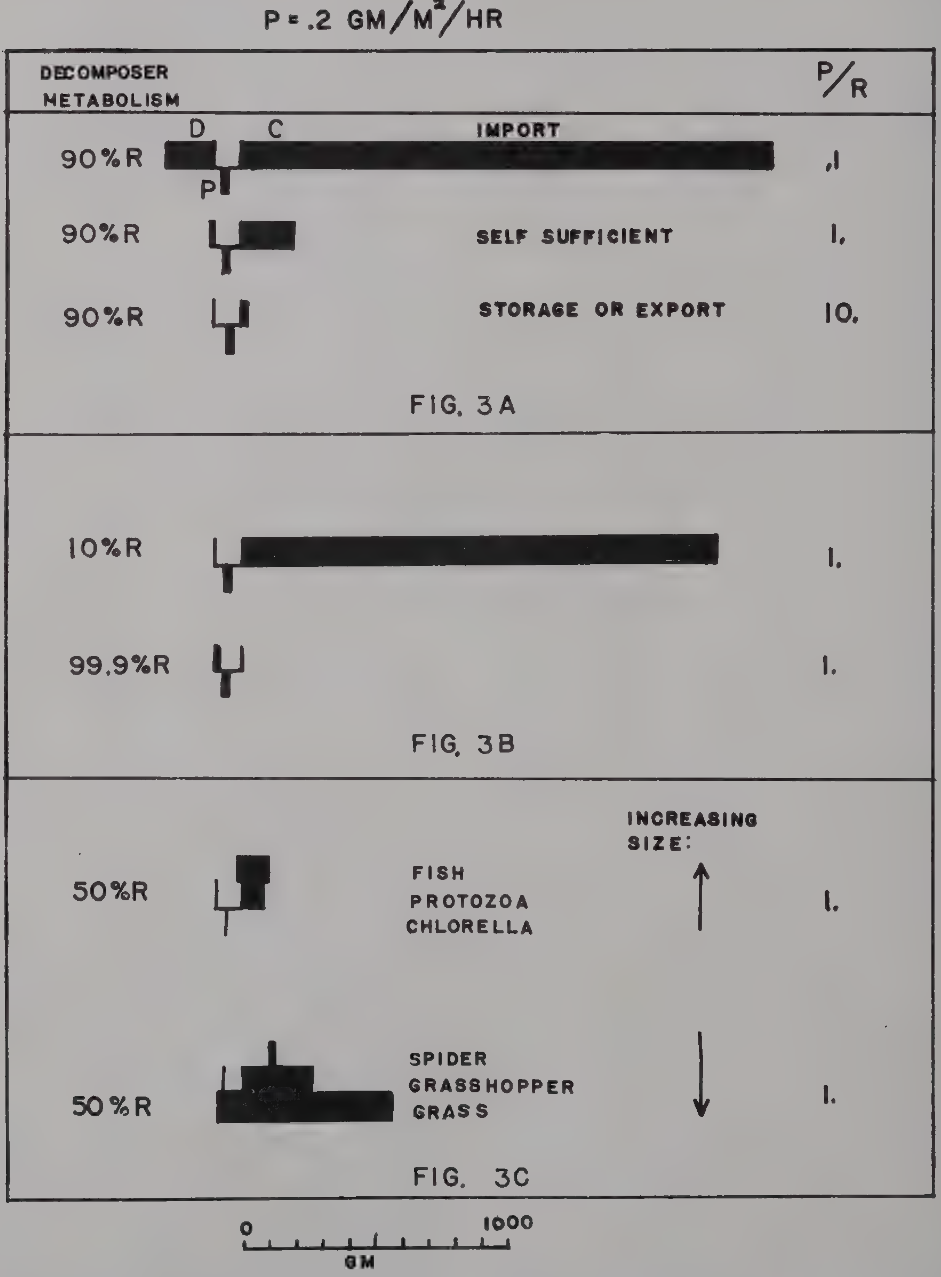

FIG. 3. Biomass pyramids (grams dry weight/m^2) under steady state conditions as a function of export-import balance, per cent decomposers consumption, and organismal size. Each pyramid is based on the same primary production (0.2 gm/m^2/hr) on an area basis. The standing crop biomass of producers (p) is indicated to scale as the lower bar of each graph. The decomposers (d) and other consumers (c) are indicated by the two bars at the level above the producers. The third level in Figure 3c refers to the carnivores. The ratio P/R indicates the ratio of gross primary production to the total community respiration. The fraction

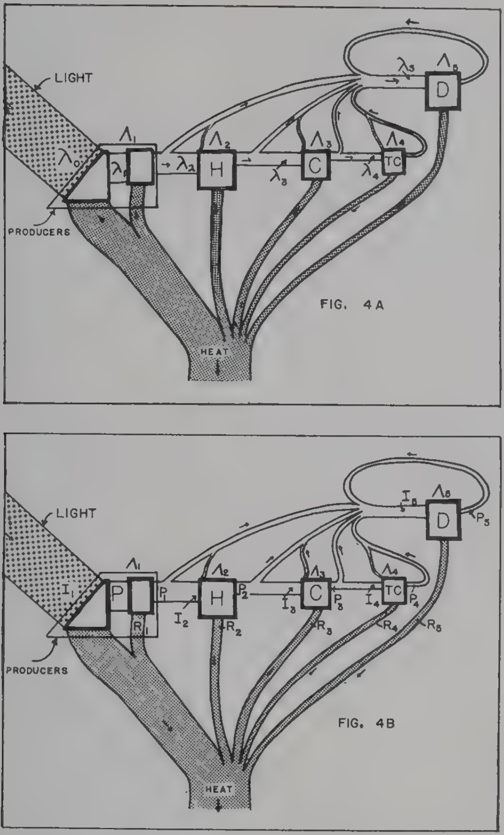

Fig. 4. Energy flow diagrams for a community with 5 trophic levels without export or import. The flow of energy into the plants as light eventually passes via shaded routes out from the community as dispersed heat. Trophic levels are represented by the heavy squares. The primary producer trophic level contains photosynthetic and respiratory divisions. The trophic levels are indicated by H, herbivores; C, carnivores; TC, top carnivores; and D, decomposers. Unshaded routes indicate the passage of energy as transferred organic matter. Production is indicated in the horizontal pathways; unassimilated consumption and decomposition routes lead upwards to the decomposers.

In Figure 4A, Lindeman's use of Hutchinson's symbols are given (see text). In Figure 4B, I_n represents energy intake; P gross primary production; P_n net production; R_n respiration; and Λ_n the standing crop of trophic level n.

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of the total respiration due to decomposers (bacteria) is indicated on the left column. Estimates of bacterial metabolism rates were taken from Figure 2.

3a. The relative dominance of consumers in the standing crop is quantitatively related to the P/R ratio. Nonbacterial consumers of the same organismal size as the producers were assumed.

3b. The relative dominance of conspicuous consumers is quantitatively related to the percent of the respiration due to bacteria. Nonbacterial consumers of the same organismal size as the producers were assumed.

3c. The shape of biomass pyramids is controlled by the distribution of organismal size in the food chain because of the increasing metabolism per gram with decreasing size shown in Figure 2.

GAP PHASE REPLACEMENT IN A MAPLE-BASSWOOD FOREST

A maple-basswood forest was surveyed northwest of Minneapolis, Minnesota, in which there was a mosaic of patches containing varying proportions and densities of saplings and seedlings which indicated that the forest canopy was being replaced in a gap phase fashion as outlined by Watt (1947). The forest is in an area (T. 12 N, R. 22 W, S. 16 SE:SE) which is a part of the Big Woods studied by Daubenmire (1936), and is approximately 60 acres in size. Although a few old stumps were present, there were no weedy herb species and the forest had been undisturbed by cutting or grazing for many years.

The author wishes to thank members of the Botany 50, 130, and 131 classes of the University of Minnesota for their help in the random pairs sampling, Brother Robert Staub for help in the sampling of seedlings, and Dr. D. B. Lawrence for criticizing the manuscript.

To test the presence of gap phase reproduction, samples were taken in the forest during the autumn of 1955. Seven random pairs surveys (Cottam and Curtis 1949) using an exclusion angle of 180 degrees were made with 40 points in each survey for a total of 280 points and 560 trees. Saplings (any stem between 3 inches and 12 inches in circumference) were measured for frequency and density by taking the four closest saplings to each point in the random pairs surveys. Density of saplings per acre was determined from 40 circular quadrats, each 20 meters in diameter, and from 33 square quadrats, each 10 meters on a side. Seedlings were sampled for frequency and density in 200 square quadrats, each 1 meter on a side.

The composition of the trees, saplings and seedlings for the forest as a whole is shown in Table I. Table II shows a breakdown of the tree data into basal area size class intervals. The forest is dominated by *Acer saccharum* which has an importance value (in the sense of Brown and Curtis 1952) of 192.4. The presence of trees of *Acer saccharum, Tilia americana,* and *Ulmus americana* in all basal area size classes of Table II, and as saplings in Table I indicates the forest might be approaching a stable, self-reproducing community.

Table I. Quantitative composition of trees, saplings and seedlings of Diamond Lake Forest

Species	Trees			Saplings		Seedlings	
	% ΣF	% D	% Dom.	% ΣF	% D	% ΣF	% D*
Acer saccharinum	.2	.1	.05	...	...	...	...
Acer saccharum	63.0	71.1	58.3	78.2	86.4	43.8	60.6
Amelanchier sp.	...	...	...	...	...	.7	.2
Carya cordiformis	4.1	2.8	2.6	.7	.3	36.9	15.3
Celtis occidentalis	...	...	...	.7	.2	...	...
Fraxinus nigra	.5	.3	.03	...	...	.7	.2
Fraxinus pennsylvanica	1.7	1.2	1.7	...	...	.7	.2
Ostrya virginiana	3.6	2.8	.05	8.7	4.9	...	...
Quercus borealis var. *maxima*	5.9	4.3	9.9	...	...	11.5	4.6
Tilia americana	8.2	6.2	13.7	5.1	3.7	...	.
Ulmus americana	8.2	7.5	8.3	2.9	2.5	3.8	16.9
Ulmus rubra	4.3	3.6	4.0	3.6	1.9	1.5	1.8

*% ΣF=per cent sum of frequency, % D=per cent density, % Dom.=per cent dominance (basal area). Nomenclature as in Rosendahl (1955).

If, however, future forest composition is based upon relative seedling importance, a slightly different composition would be predicted, and this prediction would probably be in error. For example, *Carya cordiformis* which had 1337 seedlings per acre and *Quercus borealis* var. *maxima* which had 402 seedlings per acre made up one-fifth of the seedling reproduction yet had a per cent density of saplings of .03 and .00, respectively, which is much less than the density of their mature trees.

Table II. Distribution of trees by basal area size class intervals

Species	11.5-50	51-100	101-150	151-200	201-300	301-400	401-600	601* +
Acer saccharinum	.			.			1	.
Acer saccharum	167	105	39	21	24	16	24	2
Carya cordiformis	1	5	4	4	2	..		.
Fraxinus nigra	..	1	..	1	..	.	.	.
Fraxinus pennsylvanica	1	1	..	2	2	1	..	.
Ostrya virginiana	16	..	..	..	..	.	..	..
Quercus borealis v. *max.*	1	2	..	5	4	2	9	..
Tilia americana	2	1	3	2	10	4	11	2
Ulmus americana	19	5	1	5	6	3	1	2
Ulmus rubra	6	3	5	..	4	..	2	..

*Basal area intervals in square inches at breast height.

The seedlings of these two species, which come from large nuts with abundant food, never had more than 3 or 4 leaves; *Q. borealis* usually was less than 6 inches in height, with 2 leaves, while *C. cordiformis* seedlings were rarely over one foot in height. The high densities of the seedlings of these species and the almost complete lack of saplings indicates that although the seeds are able to germinate, the seedlings cannot survive, perhaps because of the low light intensities under the dense closed canopy.

In the future, the old trees of *Q. borealis* will die and it is likely that no replacement will take place. The appearance of a canopy gap over an area with *Q. borealis* seedlings would probably not be followed by oak saplings or trees since the seeding in of *Acer saccharum* would quickly overtop and shade out the slowly growing *Q. borealis. C. cordiformis,* however, will probably remain in the stable forest since it has a few saplings which could reach the canopy if an opening were to appear.

The two species of ash did not have any saplings in the samples, but did show a low importance of seedlings. These seedlings have a chance of becoming saplings in the more open sloughy areas of the stand, although *Acer saccharum* seedlings were present in the sloughs.

The understory tree, *Ostrya virginiana,* while showing sapling reproduction, had no seedlings and is likely to decrease in importance.

Tillia americana showed no seedlings in the samples (only 2 *Tilia* seedlings were seen in the forest) and, as was noted by Daubenmire (1936) is replaced in the canopy by stump sprouts. These sprouts grow rapidly with the death of the trunk and reach toward the canopy before *Acer saccharum* can seed into the opening and successfully compete. Observations were made in several instances of two large trunks of *Tilia* of sprout origin, which were separated by a space of from two to three feet; within this space a shallow depression with decaying roots or the remains of the original *Tilia* trunk was visible.

Ulmus americana is able to cover the small sloughy areas with seedlings, and both species of elm can seed into areas of the forest where the thin litter is brushed away by upturned roots or animal burrows and organic soil with mineral matter is exposed. The sapling data show the two species to be almost reproducing the importance level of the adult trees.

Acer saccharum is reproducing a high sapling density but its relative seedling importance is less than that of its mature trees. This is of little consequence for the future of the forest, however, since the seedlings of *Carya* and *Quercus* will rarely reach sapling size, and the maple seedlings will make up a higher proportion of the saplings.

Evidence of Gap Phase Replacement

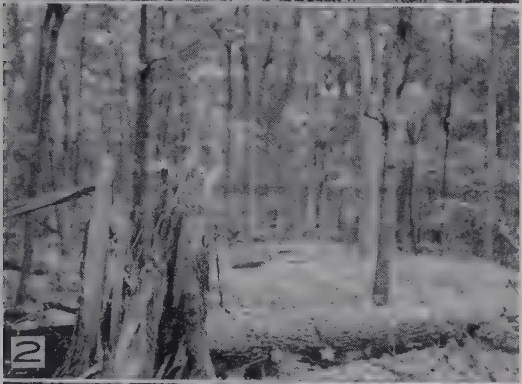
Patchiness of tree reproduction was shown from the 40 circular saplings quadrats, 14 of which had 5 or less saplings for an area of 314 sq. meters which is less than 64 per acre, while 11 quadrats had 20 or more saplings which is more than 258 per acre. Similarly, the 200 seedling quadrats showed 101 quadrats containing no seedlings while 26 quadrats had 5 or more seedlings. A Poisson test was, therefore, applied to both the sapling and seedling data to determine if the observed numbers of quadrats at various levels of numbers of individuals approximated random expectations. In both cases, there was a highly significant deviation from randomness as checked with Chi square. In the seedling data, for example, there was an expected value of 23 for the number of quadrats with no seedlings and an observed value of 101, while the expected number of quadrats with 7 or more seedlings was 2 and the observed was 21. It is therefore evident that some agency is pulling the numbers of saplings and seedlings away from a random distribution toward a more discrete situation in which there tend to be quadrats with fewer or more individuals than can be expected.

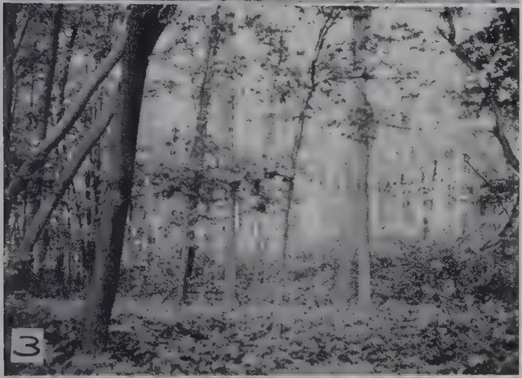
This deviation from random expectation was verified

Table III. Composition of five selected quadrats 20 meters in diameter*

Species	Totals	Numbers of Individuals				
		Q1	Q2	Q3	Q4	Q5
Acer saccharum	trees	7	5	4	5	7
	saplings	3	3	55	26	5
	seedlings	31	706	..	16	
Carya cordiformis	trees	2	..	..	..	.
	seedlings	63	16	16	16	188
Quercus borealis var. *maxima*	seedlings	16	..	..	31	..
Tilia americana	trees	..	..	..	2	
Ulmus americana	trees	2	1	..	..	.
	saplings	..	..	..	..	2
	seedlings	..	16	..	..	31
Ulmus rubra	saplings	..	..	1	.	..
Total basal area of trees....		831	289	286	1148	554

*Tree, sapling and seedling data are for numbers of individuals per circular quadrat. Seedling data was converted from number per 20 square meters to number per 314 square meters.





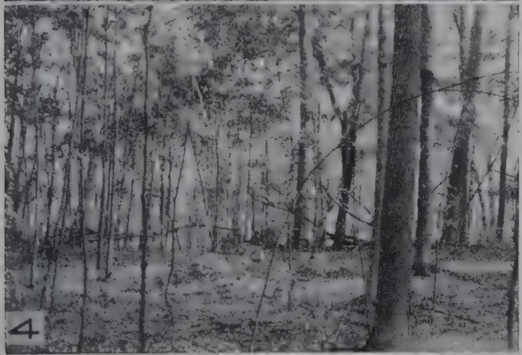


Fig. 1. A dense canopy with few saplings or seedlings which forms the continuous phase within the mature forest. Fig. 2. A wind-snapped *Tilia americana* within the continuous phase. Fig. 3. A gap, toward the right and center background, in which there is heavy *Acer saccharum* seedling production and no saplings. Fig. 4. The gap is closing with a high density of maple saplings and only a few scattered seedlings.

by numerous field observations which showed that the forest floor did not have a uniform suppressed layer of saplings and seedlings as is often supposed, but rather showed matrices where the floor was almost bare of reproduction which surrounded gaps of high density. The saplings, for example, showed a matrix (24 of 40 quadrats) where the reproduction was less than 160 saplings per acre in a forest in which the number of trees per acre is 163.6. This matrix surrounded gaps in which the density of saplings was as high as 721 per acre.

To further analyze the composition of the various gap phases, 5 circular quadrats, 20 meters in diameter, were laid in areas which seemed to conform with the various phases. It was necessary to choose the location of the quadrats since a random laying of quadrats, as was done in the original sampling, would, in part, lay quadrats across the fairly distinct boundaries of the phases.

The data from the 5 quadrats is shown in Table III. The quadrats are arranged in an approximate sequential order beginning with the mature canopy at the left and proceeding through openings of increasing age. The first quadrat shows a matrix plot with a high sum of basal areas for its trees and has few saplings or seedlings. In Quadrat 2, an opening has appeared in the canopy and there is a heavy seedling density but, as yet, few saplings. In Quadrat 3, the seedlings have matured into saplings with a density of 721 per acre. This phase often has a more complete shading effect than that of the mature canopy, and there are only 202 seedlings per acre and a decreased herb cover. Quadrats 4 and 5 show phases of the maturation of the saplings into adult trees with the restoration of a higher sum of basal areas and an increase in seedlings. In general, observations of the forest floor suggest that, except in the canopy gaps, there were few *Acer saccharum* seedlings and that in the matrix surrounding the gaps there were more seedlings of *Q. borealis* and *C. cordiformis* than of *Acer*. This indicates that *Acer saccharum* does not establish seedlings extensively in the dense shade of a stable forest in which it is the dominant species, at least, not to the extent as that of other species which are less climax but have much heavier seeds.

The ability of *Acer saccharum* to take advantage of canopy openings and to remain the dominant member of the forest seems to be dependent on its extensive seed production and the ability of its seedlings to grow rapidly in gaps and overtop the already present *C. cordiformis* and *Q. borealis* seedlings. This rapid growth and overtopping probably takes place even when *Carya* and *Quercus* have a start of several years during periods of poor maple seed production. Data on annual height growth for the different species under a mature canopy would be very helpful.

Figures 1 through 4 show four phases of canopy replacement. In Figure I there is a dense canopy and a fairly bare ground surface. Figure 2 shows a wind snapped *Tilia,* one of about 30 large trees of *Acer saccharum, Quercus borealis* and *Tilia americana* which were downed by wind early in June of 1955. Figure 3 shows, towards the right and center background of the picture, a gap with a complete cover of maple seedlings which were of a uniform height of from 2 to 3 feet. In Figure 4, there is a sapling phase in which there are few seedlings and a marked decrease in herbs.

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THE STATUS OF PLANT ECOLOGY AND PLANT GEOGRAPHY

The scope of ecology has been analyzed recently by Egler (1942), Odum (1953), Dice (1955), Mason and Stout (1954), McMillan (1954), and others. It is apparent from these writings that ecology has occupied a number of positions within biology and that the status of ecology with respect to geography has been particularly difficult to determine. The following ideas suggest that ecology is a subject matter which bears the same relationship to geography as does taxonomy, physiology, morphology, or genetics. The comments of John Davidson and Warren H. Wagner have been helpful in revising this presentation.

In a recent textbook, Odum (1953) has illustrated biology with a "layer cake" composed of five basic layers: 1. morphology, 2. physioolgy, 3. genetics, 4. ecology, and 5. etc. If this cake presentation is compared with the seven points of view in botany given by Egler (1942), a similarity is noted in the treatment of morphology, physiology, and ecology. Genetics as a layer of the cake would include the subject matter given by Egler as the study of speciation, with or without that part of genetics, which Egler has included in physiology.

Three additional subject matters—paleobotany (or paleontology), geography, and taxonomy—presented by Egler should seemingly comprise the "etc." layer in the biological cake. However, since paleobotany (or paleontology) involves chronological reference points and would include physiology, morphology, ecology, genetics, and taxonomy of the individuals which occur at any point in time, its maintenance as a layer in the cake would be as a highly inclusive one. Paleobotany might be represented best by a chronological series of five-layered biological cakes.

Of the two remaining subject matters, taxonomy and geography, the former can occupy the "etc." layer alone, but if it does, the position of geography within the series of subject matters and within the cake needs clarification.

In cutting the biological cake, Odum has indicated the vertical slices through each of the five layers as delineating bacteriology, ornithology, mycology, entomology, etc. This particular arrangement within the cake involves phylogenetic groupings. The cake could equally well represent the present arrangement of the world's biota and if so, each slice could represent an areal slice of biota. The cakes then might be compared with the subdivisions of botany as presented by Egler. The cake with the phylogenetic groupings would be likened to the subdivision, floristic botany. The cake without the prearranged groupings could be likened to the other subdivision, vegetation science (or biota science). In both cakes, the same individuals would be included; and, in either cake, a very thin slice would represent the individual.

By asking a series of questions concerning the status of the individual within the thin slice, the relationship of that individual to the various layers of the cake can be clarified. Through this analysis, the position of geography can be established with respect to the five layers of the cake.

The first question usually asked about an unknown individual by a group of students is: "What is it called?" or "What is its name?" This is not unlike the first question which is asked in a social gathering upon the entrance of a stranger. The question is prompted by the need for identifying the stranger, and the application of any symbol for identification will satisfy this need. The symbol need not denote any known relationship to any other individual. In the case of this unknown individual, the symbol *"onyma"* will be used when referring to this particular individual only.

The next question which is usually asked by students about an unknown individual is "Where did it come from?" or " Where does it grow?" Some aspect of the geography of the individual is the object of the question. The answer, *"Onyma* is from the South American Pampas," clearly establishes the geographical orientation in a particular habitat.

Identification and geography provide an introduction to biota. Rather than representing separate layers of the biological cake, they provide the platter on which the cake can be placed. The unlabeled platter is illustrated in Odum's textbook.

After the platter is provided and there has been an introduction to a biotic problem, the individual *onyma* can be investigated by means of one or more of the five subject matters or layers. The first three layers of the cake are placed on the platter when the question, "What is it?", is asked, for the answer involves an investigation of *onyma* genetically, physiologically, and morphologically. The fourth layer, ecology, is added with the question, "What is the interaction of *onyma* with its environment?", and its subsequent investigation. When the question, "How is *onyma* related to another individual?", is investigated, the fifth layer, taxonomy, is added to the cake.

Although symbols for identification and geographical orientation are vital to taxonomy and ecology, it must be emphasized that they are not an integral part of these disciplines. In physiology, a worker may report on investigations of the auxins of pea roots. Whether the plant that was studied was related to individuals placed by others under the symbol "pea" is a taxonomic problem. The physiologist has identified the plant which he investigated and has defined its whereabouts geographically. Unless the physiologist has applied the symbol to the individual by some standard technique, documentation is just as vital here as it is within any other layer-science. In genetics, a worker may try to hybridize an individual of elk grass from California with an individual of Indian grass from Nebraska. Whether the plants involved in this hybridization are grasses in the taxonomic sense of relationship is beside the point. The identification and geography were basic to the investigation. The morphologist investigating a shoot apex of ginkgo from a tree on Euclid Street may not suggest in his paper that the location of the plant was precisely that, but it was under the conditions of the Euclid Street habitat that the ginkgo apex developed as reported.

The intimate relationship of the platter to the layers of the cake is adequate assurance that identification and geography will be included in courses of any one of the five subject matters. Furthermore, sufficient interrelationship is present among the five subject matters that none will be completely separable from the others. To determine the status of ecology and the other four subject matters with respect to identification and geography (the "basic platter"), a survey of botanical curricula in 43 of the 48 state universities was made, using information available in general catalogues (1953-1956). Particular attention was given to plant ecology and plant geography courses.

While there was a certain amount of latitude in labeling, courses both in plant geography and plant ecology were offered in almost half of the departments surveyed. At one university, one plant ecology course and nine plant physiology courses were listed under a general heading of plant physiology. At the same institution plant geography was placed under the heading of plant morphology and taxonomy. One of the 43 departments offered work solely in plant geography, and seven departments offered no course in either plant ecology or plant geography. Courses in both floristic plant geography and ecological plant geography were among the offerings at one university.

While there is no assurance that courses presenting the same general subject matter at different universities will have the same content, there is a greater possibility that courses in plant physiolology or courses in plant genetics will have a greater similarity than courses in plant ecology. The bases of this assumption are the differences of opinion regarding the nature of ecology, which are frequently referred to in the literature (Dice 1955). A review of most ecology courses, however, would show a potpourri of geography, identification, meteorology, pedology, physiology, morphology, genetics, and taxonomy as well as ecology and certain other selected subjects. The content of certain courses is reflected in a recent review by Birch (1955) in which he reported that "here are some elements of ecology, physics, chemistry, plant physiology, animal physiology, pedology, oceanography and a little animal behavior (but no genetics)." Birch has expressed a common desire when he further contends that it is "time that ecology . . . decided to become a more definitive science, instead of being the poor relation borrowing from all."

The realm of plant ecology can be separated from that of plant geography. Much that is referred to as descriptive ecology, as well as much that is plant sociology, is geography. If the spatial orientation of individuals in the habitat is the primary concern, this is geography —whether it is the orientation of individuals above or below the soil surface or in a liquid medium. Techniques, such as the quadrat (cited by Dice, 1955, as definitive of ecology) and the bisect, which are used for dealing with spatial arrangements, are geographical, not ecological tools. Plant geographical research (*sensu*, syneocology, in part; plant sociology, in part) regularly incorporate correlations of plants with pedological, biotic, and meteorological geography, and should be designated as correlative geography ("interpretive plant geography," Cain, 1944).. Many ecological papers report little beyond the geographical analysis. Equally regularly, sections labeled "ecology" in taxonomic papers cite nothing other than the geographical orientation of the species. In fact, the continual confusion between the realm of geography and ecology has empowered many of the workers in other disciplines to establish themselves as ecologists when their knowledge did not go beyond the basic aspects of geography.

The geographical study, rather than solving the ecological aspects of the problem, is a means of finding where the ecological problem lies and where the ecological investigations should begin (Clapham 1956).

Ecology, first and foremost, must deal with all individuals and with the problems relative to the position of these individuals in a particular habitat.

Secondly, ecology must deal with the occurrence of all individuals in populations of any size, configuration, or breeding structure and with the occurrence of individuals in communities of any size, configuration, or combination of populations.

That plant geography, in its various usages, has included what here is placed in ecology is apparent in a recent article by Mason and Stout (1954) on the role of plant physiology in plant geography. If plant geography (and plant identification) are basic to plant physiology, and if plant geography refers only to spatial orientation, then physiology is hardly basic to plant geography. Plant ecology, on the other hand, does play a role in plant physiology; and plant physiology does play a role in plant ecology, exemplifying the interrelationship of the five layer-sciences. The above cited usage of plant geography by Mason and Stout would be synonymous with the usage of floristic botany by Egler (1942) to include plant geography as well as the other subject matters. Constance (1953), in a paper on the role of plant ecology in biosystematics, has dealt with plant ecology as intended here.

In the teaching of ecology, if we could assume that all of our students had spent several years roaming through the vegetation, identifying individuals, and geographically orientating those individuals with the pedological, biotic, and meteorological aspects of the habitat, then we would be in position to plunge immediately into the problems of ecology. Since in most, if not all, cases, we do not encounter such an ideal assemblage of prepared students, our ecology courses will probably continue to be like the bride, with something borrowed (but recognized as an interrelated subject matter), something blue (until full recognition as a definitive science is achieved), something old (less than formerly, it is to be desired), and something new (more than formerly, it is hoped).

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NOTE ON THE ECOLOGY OF *LEPIOTA LUTEA*

The writer first observed *Lepiota lutea* (Bolt.) Quel. growing on the University of Washington campus in 1953 and again observed it in 1955. Specimens, collected from under a *Chamaecyparis* in November of the latter year, were preserved in the University Herbarium by Dr. D. E. Stuntz of the Department of Botany, who also corroborated the identity of the species and was very helpful in criticizing this paper.

L. lutea is of special interest for it has not previously been recorded as growing out-of-doors in the Pacific Northwest, but has been principally mentioned as present in greenhouses in various parts of the world (Rea 1922, Ramsbottom 1923, Kauffman 1924, Smith and Rea 1944, Smith 1954 and others). The few instances of reports of the appearance in nature of this mushroom are all from the more southern regions of the United States. Both A. H. Smith and W. H. Snell collected *L. lutea* in Tennessee (Mycologia 33: 570-578, 1941) as did L. R. Hesler[1] who also found it growing in deciduous woods in Florida. H. Thiers[2] has observed it many times growing on a well-decayed pine stump in Texas.

The geographic distribution of *L. lutea,* the fact that the species had not previously been reported from this area, and its survival and continued growth after an unseasonal cold spell during which minimum air temperatures ranged from —10° to —4° C. for a period of one week, all lead to the suspicion that the local environment might be an unnatural one. A consequent study of air and soil temperatures in the area of growth proved this suspicion well-founded in that an abnormal temperature pattern (Figure 1) was the result of underground steam pipes used to heat the surrounding buildings.

On two occasions (January 2 and January 9, 1956) when air temperatures were, respectively, 5° and 7° C., standard glass thermometers were inserted into the soil to depths of from 2.5 to 25.0 centimeters. The results of these measurements showed that, although vertical temperature stratification was slight, ranging from 0° to 1° C., the horizontal temperature differential went as high as 15° C., from the center to the periphery of the "warm" area depicted in Figure 1. The appearance of *L. lutea* in December and during early January was related to soil temperatures in that major growth occurred inside the 13° C. isotherm; however later on in January the growth band narrowed to the area inside the 19° C. isotherm. Along with these temperature measurements,

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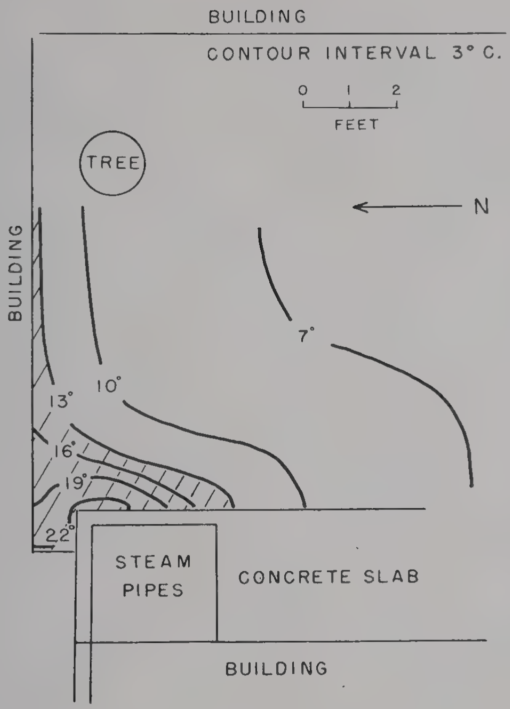

FIG. 1. Isotherms at 8 centimeter soil depth showing growth of *L. lutea* in relation to temperature.

others were made where *L. lutea* had been observed in 1953 but not in 1955, and still others away from the influence of steam pipes or buildings. Additional measurements showed that the temperature range (9° to 13° C.) at 8 centimeters soil depth in the 1953 location was somewhat lower than that within the 1955 growth area but higher than in "normal" ground (4° to 6° C.) away from steam pipe influence.

Admittedly, under usual conditions soil temperatures vary with air temperatures (Bliss 1944). But in the location examined, nocturnal cooling is prevented and the natural sequence of soil temperatures responding to air temperatures is dampened in general and almost obliterated in close proximity to the source of heat. More evidence of this was obtained on January 29 when minimum air temperatures again dropped to —3° C. At this time, temperature measurements were repeated and the presence of a climate within a climate became even more obvious than before. Very little change from previous measurements was noted in the corner close to the steam pipes, a somewhat greater change was observed farther away, but on the whole, both air and soil temperatures were higher than those outside the area, where soil temperatures at a depth of 8 centimeters were as low as 1° C.

There are probably other locations in the United States where soil composition and the pattern and magnitude of precipitation are similar to those in the southern United States where *L. lutea* grows naturally. Certainly a wide range of habitat is exhibited, since the mushroom grows in Tennessee, in deciduous woods in Florida, in association with a rotted pine tree in Texas, under a *Chamaecyparis* in Seattle, and in greenhouses where there are no trees at all. The one most apparent quality of greenhouses and of the more southern environments which is not present elsewhere to the same degree is a suitable temperature cycle for growth.

Since it is a well-known fact that climate in general and temperature in particular, often play important roles in governing the geographic distribution of plants, the manner of growth of the species in Seattle is strong evidence that temperature is a major limiting factor in the natural distribution of *Lepiota lutea*.

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THE APPLICATION OF THE CLIMAX CONCEPT TO ALGAL COMMUNITIES OF STREAMS

The applicability of the climax concept to stream situations has been broached by Eddy (1934) with reference to plankton communities and by Butcher (1946), Fritsch (1950), and Blum (1953) with respect to benthic communities. Some of these communities are comparable with climaxes of land areas in nearly every respect save in matters of size and certain structural features peculiar to algae when they grow together. An example is the *Phormidium - Schizothrix - Audouinella* community which has been described from streams in Europe (Fritsch 1950) and the United States (Blum 1953). Although this and other algal communities exhibit a considerable degree of constancy in composition and structure, the peculiarities of algal communities as they grow in streams render the applicability of terms derived from land ecology somewhat questionable.

Under land conditions in temperate and cold regions, it is unusual for a phanerogam to have a life span shorter than one year of four seasons. Hence the seasons with their variations in light, wind, humidity, rainfall, and temperature are much shorter in duration than the lives of the respective plants competing within the succession. Asexual reproduction within an algal population may occur very rapidly, however, with a generation lasting only a matter of days or even of hours, by comparison with which the algal growing season may be of long duration.

It is clear that the length of time required to attain climax conditions is dependent not so much on the length of life of the dominants as on the length of time it takes them to establish themselves among their predecessors and the subdominants, and that this establishment may conceivably be achieved in a shorter time than the lives of the dominant organisms. The duration of the climatic climax represents a fraction, usually, we may assume, a large fraction, of the duration of the climate unchanged. By the same token, the life span of the members of the climax association in terms of land ecology is some fraction of the duration of the climax.

It is likewise clear that if the lives of the organisms in the succession were sufficiently short, all stages of succession and the establishment of a climax might take place within the space of a single season. With reference to land vegetation, such a supposition is almost an absurdity, but when thallophytes are under consideration, the difficulty is real, for it is possible to construe the establishment of a complex algal community on the river bottom or in the plankton as rapid succession to a climax within a period of time characterized by diurnal changes but not by any over-all change in the climate. This is because the length of life of the individual members of the succession may bear a relation to the duration of the stabilized climatic conditions of the warm (or the cold) season similar to that which exists between the length of life of a tree or shrub of a land climax and the duration in years of the climate which determines the climax. Throughout the season which these algae find favorable, several generations may come and go before seasonal change interdicts further growth and kills off the vegetation. That these algae perennate by auxospores, a prostrate portion, hormogonia, or other means does not constitute an objection to the treatment of their vegetation as a climax any more than the production of phenomenally long-lived seeds by plants of any land climax would constitute an objection to labeling it thus. It would appear therefore that if the term "climax" is to be applied in the hydrosere, it may be necessary to include as climaxes some plant communities which are vastly more ephemeral than those occurring on land.

According to Whittaker (1953), all climaxes are edaphic, as well as topographic and climatic, but this reference presumably applies to land communities and not aquatic ones. If the aquatic environment of an alga is to be regarded as part of its "climate," then the "climate" of streams has received virtually all the attention of ecologists, to the exclusion of topographic and edaphic factors.

It seems preferable to consider edaphic factors, if they are to be regarded as existing at all in a stream, as operative mostly for those forms which inhabit sediments and have a portion of their body imbedded in the silt or mud. The forms which inhabit rocks presumably utilize the rocks only for anchorage and protection. They do not appear to exhibit preference for one type of rock more than for another, although this matter has not received serious study. The topography of the stream bottom and of individual rocks is another variable which deserves thorough investigation.

Perhaps, however, we are basically in error in attempting to foist upon the hydrosere terms such as "climate" and "climax" which were first used for land vegetation and which may, upon scrutiny, carry with them too many implications of no validity in hydrobiology. For one thing, a plant community which takes over a site and reproduces there, maintaining dominance and successfully resisting invasion so long as environmental conditions remain substantially unmodified, has fulfilled the conditions for a climax community. But, with reference to river algae, this community may not have been preceded by any other green plants whatever—colonization and dominance are thus synchronous. With no previous community occupying this site, succession has not occurred and use of the term "climax" seems inappropriate. Is it a climax—or merely a community?

We do not know as yet to what extent the atmospheric climate controls the vegetation of a stream. The river or brook may be regarded as representing a climate of its own which draws upon the atmosphere for much or all of its light, but which may be practically independent of the supernatant atmosphere in matters of temperature and water intake. Probably all intermediates occur between the small stream which is highly sensitive to atmospheric temperature change, to the large, deep, protected one which responds very slowly. Hence, it may not be assumed that the boundaries of large climatic regions have a significance for river algae commensurate with that which they have for land angiosperms, nor, without evidence to the contrary, that communities of river algae are not determined more by surface geology, depth, the trophic level of the water, or by chance, than they are by atmospheric climate.

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MINERAL CONTENT OF SPANISH MOSS

The epiphyte Spanish moss (*Tillandsia usneoides* L.) obtains all its nutrients from the atmosphere. The minute scales covering the plant are thought to aid in filtering particulate matter from the air. Nothing is known about the absorption process. The plant is well-adapted for obtaining its mineral requirements, however, as is indicated by its high ash content. In an early study, Wherry and Buchanan (1926) observed the ash content to be as high as 7 per cent of its dry weight. The ash composition was found to vary widely in plants taken from widely separated geographical locations.

The dependency of Spanish moss upon the atmosphere for mineral nutrients suggested that it might be useful in detecting air contamination in an industrial area. Contamination might be reflected by either increased amounts of normal constituents or the presence of elements not normally occurring in the plant ash.

Plants gathered near an industrial area and plants obtained 30 miles from this area were ashed and analyzed. The metallic elements were detected spectrographically and the major components were determined quantitatively by chemical means. The quantitative data were compared with data from southeastern United States.

METHODS

Spanish moss was obtained from two Louisiana locations: sample A, south edge of Baton Rouge, and sample B, Port Vincent, some 30 miles southeast of Baton Rouge. The plants were removed from live oak trees. Samples were washed in a large volume of distilled water a short time to remove adhering dust. After the material had dried to constant weight at 105° C, weighed samples were ignited in a muffle furnace at 450 to 500° C, for 8 to 9 hours.

Qualitative identification of the inorganic components was accomplished spectrographically. A Bausch and Lomb Large Littrow spectrograph with D. C. arc source was used to prepare the spectrogram. Components were identified by comparison of the spectra with master spectrograms.

In order to determine the inorganic constituents quantitatively, the ash sample was treated as follows: A weighed portion of ash was digested with aqua regia for 24 hours. The suspension was centrifuged and the supernatant was decanted. The residue was treated with aqua regia for 8 hours. The solvent was removed as before and the residue was washed with water. The washings were combined with the decantates and diluted to a known volume with distilled water. The residue (silica) was dried and weighed. Aliquots of the stock sample solution were used in the following analyses. Calcium was determined by precipitation as the oxalate and subsequent titration with standard permanganate. Magnesium was precipitated as magnesium ammonium phosphate from the filtrate obtained from the Ca precipitation. After filtration, precipitated magnesum ammonium phosphate was dissolved and reprecipitated. This precipitate was ignited to magnesium pyrophosphate. Iron was determined by the usual *o*-phenanthroline spectrophotometric procedure. Manganese was analyzed spectrophotometrically as MnO_4—after persulfate oxidation.

Sodium and potassium were determined by the flame spectrophotometric method (Beckman Model DU spectrophotometer with flame attachment).

RESULTS AND DISCUSSION

Spectrograms of both samples indicated that the same constituents were present: Na, K, Ca, Mg, Zn, Mn, Fe, Si, and Al. It was impossible to find spectral lines for Ni, Co, Cu, Cr, V, Mo, and Sn. This indicated that these elements were absent or present in such small amounts that they were lost in sample preparation.

The quantitative results are included in Table I. It is evident that SiO_2 (silica) is the major constituent of both samples although the two samples differed greatly in the amount present. The values are appreciably higher than those of Wherry and Buchanan (1926) for Spanish moss from southeastern United States. They obtained SiO_2 values ranging from about 26 to 39% of the ash. Since the ash was extracted only with acids, the Al would not be dissolved. The SiO_2, therefore, is contaminated with an unknown amount of Al.

TABLE I. Mineral composition of Spanish moss and its ash

Constituent	PER CENT OF ASH			GRAMS PER 100 G. DRY MOSS	
	A	B	C*	A	B
Ash	....	....	....	5.7	7.1
Iron	1.71	1.91	10.4	0.098	0.14
Manganese	0.50	0.33	...	0.028	0.023
Calcium	9.98	4.28	7.8	0.57	0.30
Magnesium	3.47	2.10	4.4	0.20	0.15
Sodium	5.25	1.6	2.6	0.30	0.15
Potassium	8.5	5.3	8.7	0.48	0.38
Silica	41.2	66.6	33.9	2.4	4.7

*Average of analyses by Wherry and Buchanan (1926).

Wide differences between the values obtained by Wherry and Buchanan (1926) and workers in this laboratory are noted when comparing the data for other components. The values of 1.71 and 1.91% Fe are much lower than the 10.4% (average) obtained by the aforementioned investigators.

Lack of close agreement with the previous work is noted also when the analyses for the alkali and alkaline earth elements are compared. The Ca and Na values were outside the maximal and minimal values of Wherry and Buchanan. Sample A contained about twice as much Ca and Na as did sample B. The Mg composition was lower than that reported earlier, whereas the K contents reasonably corresponded to each other.

The majority of the air-borne mineral matter obtained by these epiphytes probably is derived from soils in the surrounding area. This hypothesis is based on the assumption that surface winds would carry larger amounts of soils from the immediate area than of those from a greater distance. The soils of this area are of alluvial origin and were deposited sometime during the Pleistocene epoch. The clays and silts, in the form of complex silicate structures, contain large amounts of Al, SiO_2, Fe, Ca, Mg, K and Na; many other elements are present in smaller quantities. In this particular region of Louisiana, Mn is present in unusually high amounts. Chlorosis due to Mn toxicity is not uncommon in certain seasons of the year.

The presence of Mn in Spanish moss was not indicated by previous workers. Although a common (and essential) constituent of plants, the amount present is usually less than 100 ppm (Monier-Williams 1949). The values obtained for the moss were 234 and 285 ppm (dry weight basis). It is possible that the high Mn content of native soils is responsible for these comparatively high values.

Although zinc was detected spectrographically, it was not determined quantitatively.

From the data obtained, it was not possible to use Spanish moss to detect industrial contamination. In fact, the moss obtained near the industrial area contained less total ash than that gathered 30 miles from this location. The ash from the polluted area did contain, however, higher concentrations of Ca, Mg, Na, K, and Mn on a percentage basis. Such differences may not be significant. Comparison of the composition with that reported by earlier workers in another region suggests the differences may be due to the soil composition in the immediate vicinity. Climatic factors, including rain and wind, might possibly affect the amount of inorganic nutrients available for assimilation by the plant. These data stress a high degree of variation in the mineral composition of Spanish moss.

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SPRUCE-FIR, MAPLE-BASSWOOD COMPETITION IN ITASCA PARK, MINNESOTA

During the summers of 1939 and 1940, Buell and Gordon made a study of the relation between the maple-basswood (*Acer saccharum-Tilia americana*) and the spruce-fir (*Picea glauca-Abies balsamea*) forests in Itasca Park, Minnesota (Buell and Gordon 1945). We then found that the spruce-fir was or had been definitely the more aggressive of the two. Among the evidence was the ability of the conifers to establish themselves in dense, small stands locally throughout the hardwood forest. Once established, these "islands" became essentially exclusive of typical hardwood forest ground cover and reproduction. In commenting on these "islands" we wrote: "These islands are isolated bits of young fir forest of varying size, usually 15 to 30 meters in diameter. Maple-basswood reproduction and ground cover is excluded from them in the same way as it is from the continuous spruce-fir forest. Conceivably if additional such fir islands can establish themselves and hold on, it would ultimately result in a conquest by infiltration. But the conditions under which such islands become established and how persistent they may be have yet to be determined."

However, it has been observed in recent years that the fir islands are no longer conspicuous features in the maple-basswood stand; the fir trees have been dying out. The following is written from notes made in July, 1955. The "island" that was the principal subject of this examination was a very well established one in 1940 and was the one which provided the data for Figure 3 in the paper by Buell and Gordon (1945).

In 1955, there were 10 living fir trees in the "island," 6 dead standing fir trees, and 19 fallen firs lying on the ground and not much decayed. The latter appear to have died and then, weakened at the base, had fallen over. The largest standing fir was a vigorous tree 7.5 inches d.b.h. with 49 growth rings. Its top was well up through the canopy of the hardwoods. The others were suppressed. Two other fir trees from which increment borings were taken were 2.7 inches d.b.h. with 36 growth rings and 2.2 inches d.b.h. with 49 growth rings. Both were overtopped by the hardwood canopy.

There was an occasional fir seedling 2 to 3 inches high and two spruce seedlings the same size. What was especially noticeable was the relatively continuous presence of the typical hardwood forest herbaceous flora. Sugar maple seedlings were common throughout. But at the time the fir "island" was vigorous, maple-basswood ground cover and reproduction were extremely sparse.

Nearby were the remants of a second fir "island" with 4 fir trees still living, 3 dead and standing, and 6 lying on the ground decaying but still readily recognizable. Elsewhere in the maple-basswood stand evidence of the former fir "islands" had largely disappeared except for occasional fir trees that represent the successful survivors.

The failure of the "islands" to perpetuate themselves under the environmental conditions prevailing since 1940 has been demonstrated. No new "islands" have become established. Whatever the conditions were that allowed the establishment of these "islands," they have not been repeated in the last 40-50 years.

The "islands" have resulted finally in scattered surviving firs established among the deciduous trees, but the recent developments rule out the possibility that spruce-fir forest is at present able to invade and supersede maple-basswood.

On the other hand, it is not safe to conclude from the displacement of the fir "islands" by the hardwood forest community that the maple-basswood is able to invade the spruce-fir forest in general. The two forests exist side by side now with rather sharp boundaries. Kell (1938) suggested that minor differences in soil texture determine where each will hold control. But the soil differences are slight, and presumably, in this tension zone between hardwood and conifer forest, minor climatic fluctuations will from time to time favor one community and then the other. There will be invasions and retreats and fluctuations of boundaries. It sill remains for future study to reveal the real answer but it now seems doubtful that either of these self-perpetuating upland forests has the potentialities of advancing into and superseding the other under the existing climatic regime.

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THE HELICOPTER FOR TROPICAL BOTANICAL FIELD WORK

The helicopter has possibilities as a new tool for botanical field work in the study of vegetation in the tropics, such as for rapid transportation to inaccessible areas, for aerial surveys, and for identification of plants from the air. There are certain limitations, particularly the expense, but some of these may be only temporary.

Nearly thirty years ago, Warren G. Waterman studied and photographed vegetation of sand dunes in Michigan from an airplane. During World War II, airplanes were employed for botanical surveys, and especially, the science of photo-interpretation or analysis of aerial photographs and maps, or air-photos, expanded rapidly. For example, Jenkins (1945) cited several examples of aerial botanical surveys of military value and suggested applications, such as obtaining a general view of an area, locating representative samples for ground study, and surveying tropical forests and swamps where travel by land is difficult. Later, with the airplane, he surveyed the oil-bearing palms of Venezuela (Food and Agriculture Organization 1949).

In recent years, helicopters also have been tried by plant scientists for aerial surveys, spraying crops with insecticides, reseeding burned areas, and transporting men and equipment to forest fires. A botanist on military duty collected on mountain peaks by this means. The United States Forest Service has used helicopters since 1947, principally in fire control but also experimentally in forest survey, insect, and disease investigations. Numerous commercial applications have arisen, and optimists predict that the family helicopter of the future may become as commonplace as the family automobile of our generation.

It was my good fortune to work[1] with a small helicopter for two weeks (twelve consecutive days, each with about two hours in the air) in October 1955 with soil scientists of the University of Maryland making a reconnaissance soil survey of a coastal plain strip of about 2,000 square miles in northeastern British Guiana. The helicopter was employed primarily for transportation in the coastal swamps. Much of the vegetation is herbaceous swamp of several types, resembling the Everglades of southern Florida and composed of dense sedges and other aquatic plants rising 3 to 5 or even 8 feet above standing water 1 to 2 feet or more in depth (Fig. 1). Large areas of swamp forest are interspersed.

My work as botanist with the University of Maryland in British Guiana included classifying and mapping the vegetation and assisting the soil scientists in correlating plants and soils to increase the accuracy and speed of the survey. First, I studied the vegetation on the ground, or rather mostly in the water, at both ends of the strip, part of the time with soil scientists making a detailed soil survey of a smaller area. Specimens of the common plant species were collected for identification. Next, I made a preliminary vegetation map of the area by photo-interpretation with stereoscope of standard air-photos, scale 1/30,000, and transferred the vegetation to base maps, scale 1/50,000. Then, two weeks with the helicopter over the area gave me the opportunity to check and revise quickly the vegetation map and to study plant-soil relationships with the soil scientists at many representative localities. Field work with the helicopter continued after the termination of my assignment.

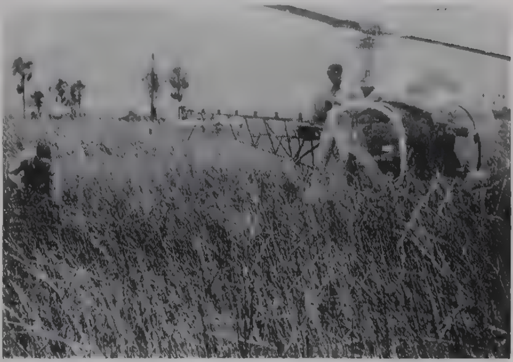

FIG. 1. Taking soil samples by helicopter in a herbaceous swamp of small bisibisi (*Eleocharis interstincta*). In background are taller sedges or razor-grass (*Lagenocarpus* sp.) and ite palm swamp (*Mauritia flexuosa*).

In size and engine, a small helicopter is comparable to an automobile, weighing less than a ton and having a 200-horsepower gasoline motor, but the cost of this complicated machine is many times greater. Not only is an airplane pilot with special training required, but also a special mechanic for daily inspection and frequent servicing. This small helicopter carries a maximum load with full gasoline tanks of about 550 pounds, including weight of pilot and either two passengers with a minimum of equipment or one passenger with more material. Cruising range is about 200 miles or 3½ hours at a speed of 60 to 70 miles an hour.

Obviously, the helicopter can provide rapid transportation to inaccessible areas for botanists in tropical countries where ordinary travel by boat, mule, or foot is slow or difficult. A small open area or clearing, even with dense tall herbaceous vegetation, will serve as a landing field. Equipped with pontoons or rubber floats, the helicopter can land also in swamps or on water. Much travel time is saved, since a locality 100 miles distant can be visited and the return trip to the base made the same day. Or, several areas can be examined in one day. A special feature is the opportunity to see and make comparisons of different places and conditions quickly, easily, and accurately in the field when fresh in the mind, instead of later reliance on memory and notebooks of studies at different times.

For surveys from the air, the helicopter is especially good, providing quick aerial views of large areas in preliminary reconnaissance. In mapping vegetation or other features from the air when air-photos are not available, the helicopter is valuable. It is superior to ordinary fixed-wing airplanes in its slower speed, its ability to fly safely at low altitudes, and the better visibility from the transparent plastic dome. Thus, for identification of vegetation or individual plant species from the air, the helicopter is better. It is also suited to surveys of a single economic tree species for locating commercial stands and estimating potential yields.

There are also limitations, some of which may be only temporary and subject to future mechanical improvements. Landings cannot be made everywhere. Under ordinary conditions and with safety, a small loaded helicopter does not perform the feats of emergency landing, rescues, or military operations, such as use of rope ladders to the ground. The vast unbroken dense tropical forests extend many miles without suitable spaces for ground inspection or even emergency stops. Nor can safe landings be made in shrubs or on rough terrain, such as interesting collecting areas of high mountains.

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[1] As Botanist with the University of Maryland in British Guiana from August to November, 1955, under the International Cooperation Administration.

Hovering, or motionless flight, can be done best at heights within ten feet from the ground, where there is ground effect, or support from the column of compressed air beneath. A small helicopter cannot hover anywhere, such as at very low heights near the forest canopy, where it would be particularly useful in tree identification but where the down draft would blow the foliage.

Inability to carry heavy or bulky loads restricts the usefulness of a small helicopter to a plant collecting expedition. There is scarcely space inside for large plant presses, though they might be strapped outside to the frame. (I wrapped in newspapers my few botanical specimens of the common species.) However, several trips might be made to transport presses, driers, gasoline, provisions, etc., as well as guides to inaccessible sites. Likewise, round trips from a base must be restricted to points within a radius of 100 miles in the absence of refueling stations. Obviously, the present larger helicopters could transport heavier loads at proportionately less expense.

Flying is confined to periods of good weather and clear visibility in daylight. However, the helicopter can land to wait for showers to pass or detour around areas of local rain storms. Also, it functions best at low altitudes and is less suited to high mountainous regions with low barometric pressure.

Not yet readily available for hire when needed, a helicopter is subject also to delays in negotiating a contract, in delivery, and in servicing and repairs. At present the greatest limitation of the helicopter is its expense, approximately $75 to $100 a flying hour, though subject to some variation. Thus, the cost is too high for most botanical field work except where associated with a project of direct economic value or with military or defense activities. However, in time costs should be reduced through mass production.

Identification of unknown trees of the numerous species in the mixed tropical forests is difficult from the helicopter as from the ground. At the cruising speed of 60 miles an hour, naming from the air is no easier than from a train or automobile at the same speed. However, the helicopter can slow to 30 miles an hour or less, skim over the tree tops, circle and return to a particular tree, and fly slowly beside the crown (Fig. 2). Vibration is slightly greater than in an ordinary airplane and too much for use of field glasses at low elevations. Landing and close examination from the ground or collection of a botanical specimen are desirable for determination.

Once known and identified, trees of many species can be recognized from the helicopter by their size, crown shape, color tone, and texture of foliage, size and shape of leaves, color of showy flowers or fruits, etc. (Fig. 3). The different forest types can be distinguished by their dominant species. Likewise, types of shrubby and herbaceous vegetation can be recognized from the air. Identification of trees in a strange region probably could be facilitated by preliminary flights with a local man who knows the common names, just as an experienced woodsman is helpful on the ground.

When perfected, the helicopter may solve the difficult problem of collecting herbarium specimens from giant tropical trees, though now one cannot reach out and gather twigs from the air. With a special gadget, such as pruning shears or hedge clipper and basket supported from a pole, the plant collector of the future should get his tree specimens easily by helicopter. Or, he might descend from the helicopter to the tree tops by rope ladder or a hoist to obtain epiphytes as well as tree specimens.

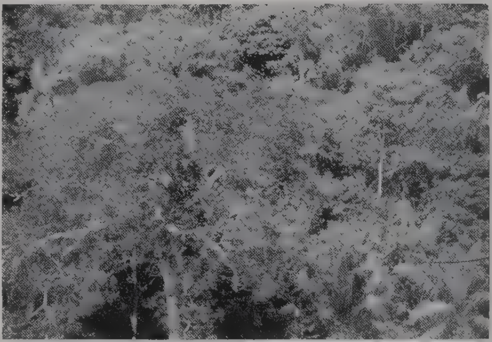

FIG. 2. Giant locust tree (*Hymenaea courbaril*) with whitish trunk and branches and thin rounded spreading crown of shiny green foliage. Cocorite palm forest with cocorite palms (*Maxmiliana* sp.) at right foreground.

The ordinary fixed-wing airplane possesses some advantages in botanical field work, doing more cheaply some of the same tasks as well as others. It can make reconnaissance flights and aerial surveys though at slightly greater heights and speeds. Heavier loads can be carried for longer distances. By landing on rivers and lakes, an amphibian plane can transport botanists and equipment quickly to less accessible localities.

Likewise, regular scheduled passenger airplane flights present opportunities for botanists to observe the vegeta-

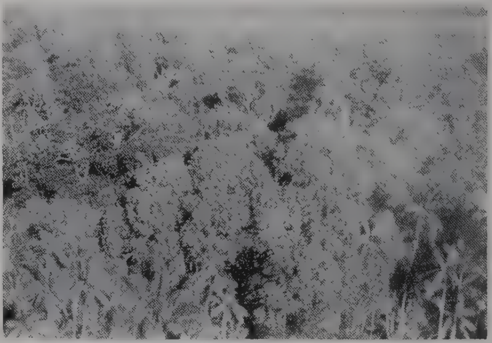

FIG. 3. *Licania* forest with several tree species readily distinguishable by differences in color of foliage, crown shape, and leaf size and shape. Examples are *Licania* sp., the dominant species, with rounded brownish crowns, common at right; locust (*Hymenaea courbaril*), also in Fig. 2; *Didymopanax morototonii*, with nearly flat crown of yellow green foliage; *Jacaranda* sp., with dark green fine foliage and showy masses of purplish flowers; and *Vochysia* sp., with shiny green foliage and bright yellow flowers beginning to open. Also in foreground are palms of two species, manicole (*Euterpe* sp.) and cocorite (*Maxmiliana* sp.). Herbaceous swamp in right background.

tion of unfamiliar regions, less closely than from the train window but with a better aerial view. Smaller planes flying slower at lower elevations and with more stops are better for observation than the nonstop airliners. Good maps, a camera, and field glasses are important accessories.

Aerial photographs as base maps summarize for field botanists much detailed information on topography, streams, culture, geology, and vegetation more accurately than could be sketched from a moving helicopter. In mapping vegetation, I would prefer air-photos to the use of a helicopter if both were not available together. Naturally, both tools should be supplemented by field work on the ground. Individual tree species can be identified much better from the helicopter or airplane than from the small scale, black-and-white air-photos. Foresters have utilized air-photos extensively in making forest inventories, and botanists might make greater use of them too in studying vegetation.

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VARIATIONS IN TEMPERATURE IN SMALL AQUATIC SITUATIONS[1]

In considering the ecology of small organisms in puddles, pools, small ponds, or restricted portions of larger aquatic habitats, the usual temperature determinations may be relatively meaningless. That is, the daily or even hourly heat regime may be more important than the annual cycle of heating and cooling. Although several investigators have considered the general problem, relatively little literature on the subject is available in English. Many types of situations remain to be investigated, and the following notes may suggest some of the problems it would be worthwhile to study in greater detail.

Small Aquatic Situations Exposed Directly to the Sun

Pichler (1939a) suggests a useful classification of small bodies of water, based on their thermal and depth characteristics:

Puddles: Small bodies of water up to 20 cm deep with bottom heated strongly by sunlight. Practically no thermal stratification during the summer. Temperature range in summer as much as 25°C.

Pools: Deeper bodies of water up to 60 cm with bottom receiving some heat from sunlight. Thermal stratification interrupted daily through a period of homothermy. Temperature range in summer: up to 15°C at surface and 5° at the bottom.

Small ponds: Larger bodies of water up to 1 m in depth in which the bottom does not receive a measurable amount of direct heat from the sun. Thermal stratification more stable but usually interrupted daily by a period of homothermy. Temperature range in summer: up to 10° at surface and 2° at bottom.

Pichler's classification is based mainly on observations made in central Europe and the temperature range and thermal stratification may differ markedly in other regions. The following records of surface temperatures of freshwater and brackish puddles and pools (about 2 m in diameter and 5 to 50 cm deep) on the Florida Keys indicate some of the extremes to be expected:

Surface Temperatures (°C at 1 cm depth) and Salinities (0/00) in Unshaded Puddles and Pools on the Florida Keys[2]

Time	*Temp.*	*Salin.*
1130	33.5	(0.29)
1300	37.0	(0.3)
1430	42.0	(0.6)
1500	38.0	(0.4)
1530	38.0	(0.4)
1530	35.0	(0.25)
1700	37.0	(0.0)
1730	38.5	(0.05)
1800	34.0	(0.0)
1800	32.5	(0.28)
1830	32.5	(0.05)

The lowest surface temperature (at 1 cm depth) recorded on the same day was 29.0°C at 1130 in a shaded portion of the first pool on Upper Matecumbe Key. Temperatures at a depth of 12 to 15 cm were generally lower, but did not exceed a difference of about 7° (42—35° at 1430); and some puddles were so shallow that the bottom temperature was identical with that at the surface. The temperatures in these pools were probably influenced to some extent by the decrease in specific heat due to the presence of salts; but, even in Indiana and Europe, surface temperatures in very shallow freshwater pools or the shallow edges of larger ponds may approach 40°C in the middle of the afternoon in July and August.

Extremes such as 42°C are close to the thermal death point of many insects, but larvae of *Tropisternus quadristriatus* Horn, a characteristic brackish water beetle, were active in the infraneuston even at that temperature on Key Vaca. Water beetles and other insects were collected at the surface in nearly every pool examined, although the vegetation (mostly *Chara* spp.) was dead, and looked as if it had been cooked, at and just beneath the surface.

With the possibility of such large fluctuations in temperature in brackish puddles and pools, it is not surprising that several water beetles ordinarily associated with brackish water occur in western hot springs (Brues 1927, *et al.*). It seems that the fauna of small brackish pools is in a sense "preadapted" to invade unusually rigorous environments. The extensive ranges of many brackish water beetles support this conclusion. *Tropisternus quadristriatus* apparently occurs from Massachusetts to Argentina along the Atlantic Coast and may be only subspecifically different from forms found in saline waters in the Rocky Mountains and on the West Coast. *Berosus metallicebs* Sharp occurs on islands off the west coast of Mexico and in the Bahamas.

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[1] Contribution No. 604 from the Zoological Laboratories of Indiana University.

[2] Records made by F. N. Young and J. S. Hager of the Florida State Board of Health, August 22, 1949, on Upper Matecumbe, Grassy, Long, and Vaca Keys. The pools examined had at one time or another been found to breed various mosquitoes.

Shallow puddles and pools in tropical regions might be expected to show even greater surface temperature variations. It has been noted in other parts of Florida that shallow rain pools directly exposed to the sun seldom contain water beetles, although adjacent ones under the shade of trees may be well populated. In some cases the pools seem to have undergone "Pasteurization" and many dead animals are found in them. On the other hand, Vaas and Sachlan (1955) and others apparently did not find surface temperatures much above 34°C in shallow fresh-water ponds in Java. The situations studied, however, were mostly deeper or much larger than those examined in Florida.

Aquatic organisms, admittedly, do not usually remain in the layers of water where maximum heating occurs. Diurnal-nocturnal migrations of plankton and other small forms have been repeatedly observed even in small pools. In Indiana, *Laccophilus fasciatus* Aube and *L. maculosus* (Say) are not found in the shallows of ponds at times of the day when the temperature at the surface approaches 40°C. They tend to concentrate under sticks and floating vegetation or burrow into the bottom. Conversely, in the early morning and at night they can be found foraging at random in the shallows.

Shaded Situations and Swamps

Pichler (1939a) summarizes work done on shaded-woods ponds by Gieysztor (1934) and von Brand (1936). As would be expected these situations show different thermal characteristics from those where direct insolation is possible. Gieysztor observes that spring temperature conditions in continually shaded woods pools persist into the summer, which correlates with the occurrence in the warmer months of many organisms characteristic of spring conditions in other situations. For example, in the southern United States the water beetles of the genus *Matus* are found mostly in the months of April and May, while on the E. S. George Reserve in Michigan they appear in the woods ponds and shaded swamps in August.

Studies on temperatures in small pools in a tamarack swamp on the George Reserve show considerable variation depending on degree of shading and depth in relation to air temperatures. The whole swamp, however, seems to respond as a unit to a rise in temperature, and even the most protected pools surrounded by hummocks and heavily shaded show a gradual rise over the summer.

Stratification, "Microthermoclines," and Temperature Reversals

Pichler (1939a, 1939b), Buschkiel (1939), Steinböck (1938), Vaas and Sachlan (1955), Vaas and Schuurman (1949), and others discuss various phenomena of stratification in small bodies of water. Steinböck (1938: 497) gives a beautiful example of a "microthermocline." Vaas and Sachlan (1955) discuss the temperature reversals during the diurnal-nocturnal cycle in shallow water and summarize Buschkiel's work. This phenomenon is apparently of considerable importance in fisheries production in Javan fresh waters.

The following interesting situation was observed in connection with algal mats on the George Reserve, June 21, 1952:

Temperatures at 1330 Over and in Algal Mat on Burt Pond (°C)

Surface of mat	21-22
2.5 cm down in mat	23-24
5 cm down beneath mat	25
7-8 cm down beneath mat	21-23
15 cm down beneath mat	20

This reversed stratification was apparently produced by direct insolation heating the surface in the morning followed by cloudiness with winds cooling the surface. The mat interferes with convection currents that would otherwise equalize the temperature. *Bidessus flavicollis* (LeC.) and *Hydrocanthus iricolor* Say are characteristic water beetles found in algal mats, but they seldom occur in small pools or in situations where no shade is present during the hotter months.

Springs and Seepages

Cold springs are often noted as the habitat of various supposedly relict water beetles and other insects. This is especially true of the *Hydroporus vilis* group (Young 1953; Chamberlain 1947) and other species of *Hydroporus.* These beetles are often active at temperatures which quickly immobilize or even kill warm-water species such as *Hydrocanthus iricolor* Say when transferred directly from warmer water. On the other hand, the cold spring species frequently die in a matter of hours when removed to warmer water.

As in the case of very warm water, however, the species which are associated with cold springs do not occur exclusively in the coldest areas or layers. Instead, they are frequently found in the lateral seepages, in submerged mosses, or even partly out of the water. Also in warm weather even the coldest springs warm to some extent. For example: A spring in which *Hydroporus pseudovilis* Young occurs showed the following variation in temperature during the summer of 1952:

Average Temperatures in G-5 Spring on George Reserve (in °C)

	June	August
Springhead	9.0	11.0
Run below spring	11-12.5	10.5-13.5
Lateral seepage	15.0	16.0

This represents a relatively constant spring, however, and smaller springs in the same area show much greater variation in temperature.

The difference in temperature between a springhead and lateral seepages is usually small, but where rain pools or other small pools are close at hand striking differences may be observed. In one of the springs on the George Reserve, the springhead remained at 9°C throughout the summer of 1952, but pools in the marsh only a few inches away were warmed to as much as 26°C in June.

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A PISTON SAMPLER FOR SURFACE SEDIMENTS OF LAKE DEPOSITS

Increasing interest in the properties of surface sediments of lake deposits indicates the necessity for an inexpensive sampler capable of taking undisturbed cores extending through the mud-water interface to depths of 50-75 cm. The Livingstone piston sampler (Livingstone 1955) and Vallentyne's modification of it (Vallentyne 1955) are admirably suited to the removal of undisturbed cores from solid and moderately compacted sediments, but both of these devices cause distortion and some loss of the flocculent sediments composing the mud-water interface and that of the centimeter or so beneath it. The Jenkin sampler (Mortimer 1942) preserves the surface layer, but is not suited to the removal of the deeper sediments. The sampler described below combines the more desirable characteristics of these devices, and has the advantage of being less expensive to construct than either of them.

DESCRIPTION OF THE SAMPLER

The sampler consists essentially of a clear plastic (Lucite) tube, 4 ft. 6 in. long, which contains a piston, and is supported by a head piece to which extension rods can be attached. Details of the design are shown in Figure 1.

The *head piece* (Fig. 1, A) has a threaded brass or steel rod (2) to which is riveted a brass ferrule (1) threaded on the inside to receive the adapter (C) of the extension rods. Two No. 10 rubber stoppers (5) are cut to fit evenly, but not tightly, into the plastic tube (6). Four aluminium discs (4) drilled as shown in the cross sectional sketch (D, 4) are mounted on either side of the rubber stoppers. The stoppers can be perforated most conveniently on a high-speed drill press at the same time as the aluminium discs are drilled, using a disc as a template. Three aluminium rods (A, 7; D, 7) with turned ends, separate the discs and stoppers. The threaded rod (2) passes through the central hole in the aluminium discs and stoppers, the aluminium rods pass through three of the peripheral holes, the piston line (8) through a fourth, and the remaining four holes permit the escape of water from the sampler as the tube slides down over the piston (B). Two wing nuts (3) complete the head piece assembly. When the head piece is inserted into the plastic tube, tightening the upper wing nut compresses the rubber stoppers vertically, expanding them laterally, thus holding the tube firmly attached to the head piece.

The *piston* (Fig. 1, B) consists of a No. 10 rubber stopper (12) cut to fit evenly, but loosely, inside the plastic tube. A chamois washer (11) covers the stopper, extending slightly beyond its lower edge. Two aluminium washers are placed one on either side of the stopper. A threaded bolt fitted with eye nuts (10) passes through the center of the piston, so that turning the lower one compresses the stopper, fitting the piston snugly inside the tube. The piston is attached to the piston line (8) by a swivel snap (9) which is fastened to the upper eye nut. Nylon-cored plastic clothes line makes a very satisfactory piston line.

The *adapter* (C) is a short brass rod threaded on one end to fit the ferrule (1). The other end is drilled to receive the extension rod, to which it is fastened by a key. Vallentyne uses one- and two-meter lengths of aluminium pipe as extension rods. These have a short piece of aluminium rod riveted into one end, and are fastened together by keys as described above. Their light weight and rigidity recommend them for use with this sediment sampler. It has been found that when surface sediments are being taken in ten meters or more of water, bowing of the extension rods may occur unless the piston line and extension rods are held together. The most convenient way to do this is by the use of open rings (13) of heavy aluminium wire, the ends of which by-pass one another, riveted to brass collars which slide over the end of the extension rods and are held firmly in place by tightening the collar screw. The piston line is inserted by placing it at right angles to the extension rod and pressing it into the ring.

A *funnel* of rubber dam fastened to the top of the sampler helps greatly in collecting samples of the flocculent surface sediments. A circular wire (E, 15) is bent into the shape of the rim of a beaker, providing a lip. It is supported by four wires (16), of the same material, fastened to a brass collar (17) with screw, which slides over the top of the plastic tube. Rubber tubing (14) slit open lengthwise is fastened around the wire ring (15) except at the lip. A circular piece of rubber dam (18) is then cemented to the tubing and around the wire lip. A hole cut in the center of the dam permits the plastic tube of the sampler to pass through. If the hole is somewhat smaller than the diameter of the tube, the dam clings tightly to the outside of the tube and can be fastened more securely by placing a rubber band (19) over it. A short section of bicycle tire tubing provides a very useful band for this purpose.

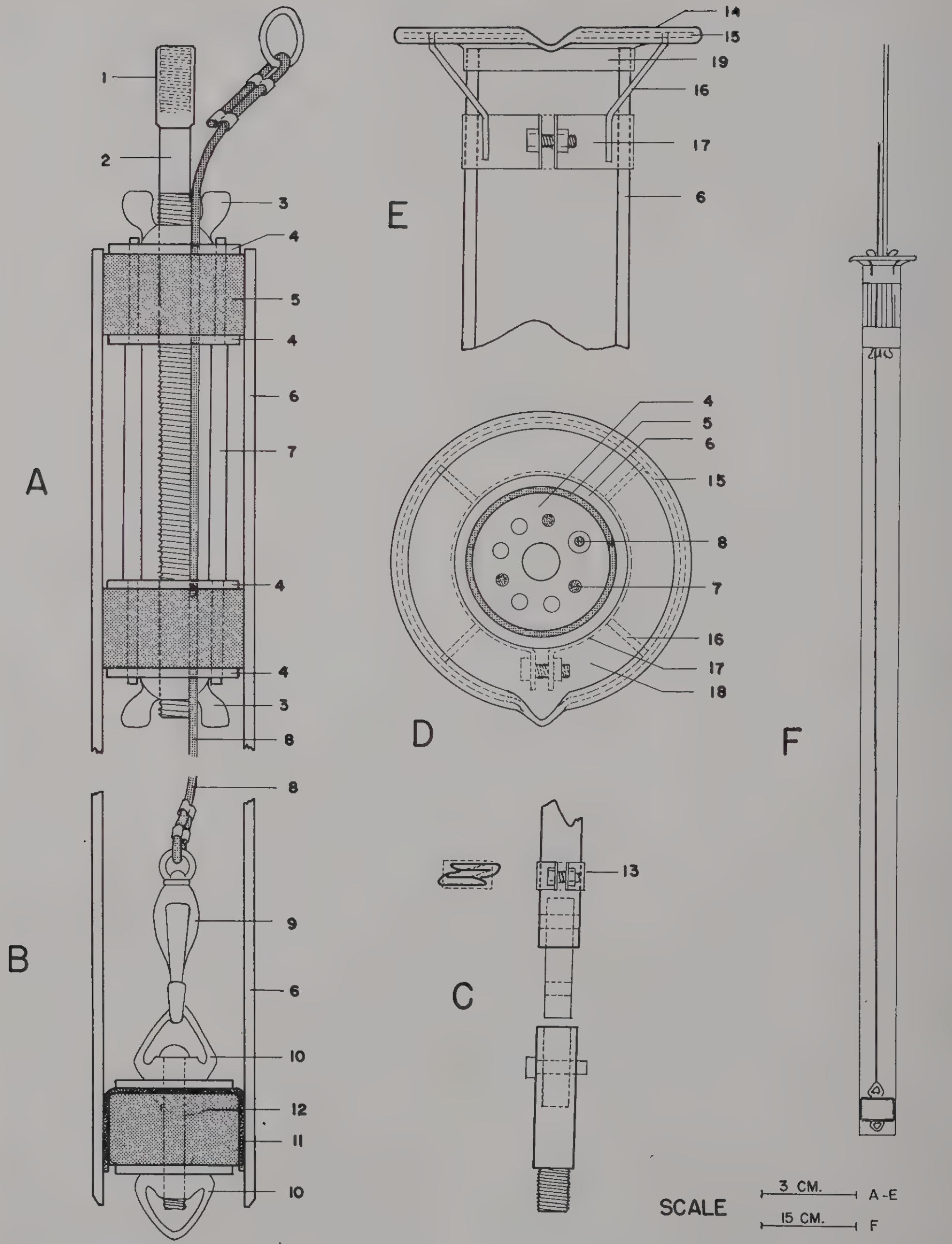
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FIG. 1. (A) Head piece, (B) Piston, (C) Adapter, (D) Cross section of sampler and funnel, (E) Funnel, (F) Assembled sampler

OPERATION OF THE SAMPLER

In order to obtain undisturbed samples of surface sediment it is necessary first to know the depth of water in the area in which cores are to be taken. If only a single core is required, it can be taken from a small boat, but if a larger number of samples is necessary a raft or platform placed across two boats is desirable.

A suitable length of nylon-cored plastic line is attached to the ring in the piston line. The assembled sampler (Fig. 1, F) is then allowed to fill with water, so that the sampler assumes a vertical position. Extension rods are fitted together as the sampler is lowered in the water, and the piston line pressed into the line guides which should be spaced about two meters apart. When the total length of sampler and rods is about 15 cm less than the depth water above the mud-water interface, the piston line is secured to the boat or raft. The extension rod is then pushed down a further distance equal to the distance between the piston and head piece, thus taking the core. The water in the sampler flows out through the holes in the head piece insuring slow, even movement of the piston and minimal disturbance of sediment as the tube moves down cutting out the core.

Sampler and core are then pulled up, the piston line removed from the line guides, and the extension rods removed as each emerges from the water. If the core is to be transported using the sampler as a container, a No. 10 stopper is inserted into the lower end of the sampler before it breaks the surface of the water, and the piston and head piece are left in the sampler. If, on the other hand, a number of cores are to be taken, the core must be transferred to suitably labelled containers. A rubber stopper the same size as the piston, mounted on a 2½-ft. extension rod, is introduced into the lower end of the sampler before it is removed from the water. The sampler, held in a vertical position, is then removed from the water, the upper wing nut slackened, and the head piece removed without disturbing the piston. With gentle pressure on the rod, while keeping the piston line taut, the core and piston are moved slowly up the tube until the piston reaches the top and is removed. A second 2½-ft. extension rod can now be fitted into the first one and the core pushed up until the mud-water interface is level with the top of the sampler tube. The position of the bottom of the core is recorded on the sampler tube with a china-marking pencil, from which point required strata are marked off unless a continuous core is desired. Further pressure on the extension rod causes the extrusion of the core, the semi-liquid surface layers spilling over into the rubber funnel, the lip of which aids in collecting the material. In this way sediment samples can be taken varying from a few millimeters to several inches in thickness. In more compact sediments a spatula can be used to cut off sections of the core.

This sampler has been used by Vallentyne and the author in obtaining cores for the study of sedimentary pigments, with very gratifying results. Stratification of sediments does not appear to be distorted in any way, and the transparent sampler tube has the obvious advantage of permitting visual inspection of the intact core, revealing characteristics which might otherwise be overlooked easily. The major disadvantage in its use stems from the time-consuming procedure of coupling and uncoupling the extension rods as each core is secured. At present no simple way of overcoming this difficulty can be suggested. A second disadvantage arises from the necessity for accurate measurement of the depth of water at the point where cores are to be taken. This can be done at a near-by location at the time of sampling if the operator is prepared to take one or two trial cores prior to more accurate sampling. In such circumstances it has been found useful to have a 4-ft. length of stiff wire at hand, the end of which is bent into a hook. This can be inserted into the lower eye nut of the piston pulling it down to its original position, thus avoiding the necessity of removing the head piece to do so.

The cost of materials and construction of the sampler may vary with locality, but is estimated at about $15.

SUMMARY

A simple, inexpensive surface sediment sampler of the piston type is described and its operation outlined. Its primary advantages are that (1) undisturbed cores of lake sediments can be taken through the mud-water interface to depths of 75 cm, and (2) by employing a clear plastic tube, it permits visual inspection of the intact core.

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A LABORATORY CULTURE METHOD FOR CRAYFISH

The crayfish has been popular as an animal for classrooms and for research, particularly in physiology laboratories. The reasons for this are many but certainly their availability is an important one. However, they are not readily obtainable in large sections during winter months. For this reason a stock was established at Washington University in St. Louis and has been maintained as a breeding population for six years. Many colleagues have written for information on the culture method; apparently the success of this stock is something less than routine and prompts this note.

It would be gratifying if the procedure outlined below had been carefully planned and assiduously administered; in truth there was no protocol. But in retrospect, success was the result of an ecological rather than a physiological point of view. The needs of crayfish were not catalogued and furnished; the first thought was simply to provide as near to an indoor pond as possible for a pond species, *Procambarus allenti* Faxon. Three provisions seem to have been of most importance.

1. The crayfish cultured was a pond species (Hobbs 1942) tolerant of environmental extremes.
2. The substratum furnished refuge for molting individuals.
3. Continuous illumination of the tank maintained a rich green flora.

The concrete tank used was approximately four by six feet. The bottom was covered deeply with crushed limestone (chat) to form a tank approximately eight inches deep. Hollow tiles, bricks and rocks were piled in the center and scattered to form refuge. With time, this substratum was covered with an organic silt; that this was foul smelling when disturbed attests to the bacterial action but no attempt was made to remove it.

Water was maintained at about a four-inch depth by a tap drip compensating for evaporation loss. It was naturally hard water, perhaps rendered more so by the limestone bottom; by standard soap test it registered "very hard." The water also became high in nitrate content. While the tank side was only a few inches above the water level, almost no escapes were made by the crayfish; this has not been the experience when dealing with glass aquaria which always require cover.

Aeration by two or more lines was continuous, the air finely divided by "air breaking stones" at the ends. The large surface area relative to volume, agitation by the animals and aeration resulted in a fairly high and constant oxygen tension.

Two light sources of 200-watt bulbs with reflector shades maintained continuous illumination. This resulted in a very rank growth of green and blue-green algae. The bricks, rocks, tank sides, and bottom silt were solidly green. *Elodea, Lemna* and other aquatic plants were started many times but were rapidly depleted by the crayfish.

Additional food was provided on a very casual basis. From time to time, sacrificed mice, frogs, and chicks were tossed in; these were quickly stripped to the bone. Every few days a handful of commercial mouse-food pellets was thrown in. Lettuce leaves were occasionally put in and immediately consumed.

These sources of food were supplemental, however, to a basic food chain. The silt and algae were rich in protozoans and small crustaceans, particularly ostracods. An accidental contamination of guppies reached a population of hundreds. These, while competing with the very young crayfish and possibly predatory on them as well, were active grazers on the algae. The continuous supply of dead fish provided food for the larger crayfish.

In this microcosm, the crayfish population numbered several scores of adults with, from time to time, numerous immature individuals. If the adults were removed for experimental use, they were replaced by the young. Breeding appeared to be fairly continuous; the numbers of berried females were sometimes very large, sometimes only one or none.

When large numbers of young crayfish were needed, they were obtained by placing a female bearing hatching eggs in a finger bowl with a coarse rock bottom. This allowed the young to drop into the interstices and escape cannibalism by the female. With removal of the adult and addition of green algae, the young were reared through two or three molts before the bowl became overcrowded and cannibalism began among the young. Here, as in the large tank, providing more places of refuge than crayfish is of great importance in the light of their aggressive behavior and need for spacing (Bovbjerg 1956).

It should be emphasized that this is not a "tried and true" culture method but a description of how one breeding population was maintained in the laboratory.

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ON UTILIZATION OF SALT WATER PONDS FOR SHELLFISH CULTURE

During the last few years considerable interest has been displayed by the members of this laboratory and several of our colleagues in the possibilities of cultivating the American oyster, *Crassostrea virginica,* and other molluscs in small, enclosed or semi-enclosed salt water bodies, such as the numerous ponds that are found along the shoreline of a mainland and also on some large islands, such as Gardiners Island, New York; Martha's Vineyard, Massachusetts; and others. This interest is shown because the oyster beds in such large areas as Long Island Sound are severely damaged by frequent hurricanes and storms, and because the efficient control of oyster enemies there is extremely difficult. These disadvantages, however, can be eliminated if oysters are grown in relatively small bodies of water that are well protected against the action of storms, and where the control of oyster enemies is more feasible (Loosanoff 1954a).

Since several groups of workers are already either engaged or planning to engage in pond work, it seems desirable to offer a definite plan to evaluate the suitability of these salt water bodies for shellfish culture. For this, the following steps are suggested:

I. Make a general survey of the ponds to determine the following:
  a. Total area of the pond and its depth at different points.
  b. Character of the bottom, and extent of areas suitable for oyster beds.
  c. Presence and condition of native oysters in different parts of the pond.
  d. Occurrence and distribution of oyster enemies.

II. Conduct the following studies, the results of which should help to manage the ponds more efficiently:
  a. Changes in salinity, temperature, and pH of the water in different parts of the pond.
  b. Quantity of dissolved oxygen at different depths during different seasons of the year.
  c. Changes in quantities of nutritive elements in the sea water, such as phosphates, nitrates, *etc.*, and changes in plankton during the summer or, if possible, during the entire year.
  d. If the pond is semi-enclosed, determine its tidal range, and direction and velocity of tidal currents.
  e. If the pond has no connection with the outside, and its currents are sluggish, consider the possibility of installing current-producing and aerating devices.

In ponds that are connected with the outside by narrow channels, the possibility of controlling the tidal flow should be considered. For example, tide gates would help to retain the larvae until they are ready to set. Such gates, or other means of preventing the inflow of sea water, and maintaining the water level at a desired height, should also be valuable in controlling certain enemies. For instance, by allowing an inflow of fresh water and by blocking the entrance of sea water the salinity of the water in the ponds can be maintained for a sufficient time at a level low enough to kill drills, starfish and, perhaps, even crabs, without seriously affecting the oysters.

On the basis of the above observations tentative decisions may be made as to:

a. Location and extent of individual spawning beds.
b. Areas of bottom that can be utilized for cultch planting.
c. Quantity of shells that can be planted on each bed, and desirability of utilizing seed-collecting methods and devices other than the planting of loose shells.
d. Methods of control of oyster enemies to be instituted.

The peculiarities of the pond would help to decide what types of seed collectors should be used. These may be either loose shells, egg-crates dipped in cement, chicken wire bags filled with oyster shells (Prytherch 1930), or several others successfully used in Europe (Orton 1937) and Japan (Cahn 1950). Bags containing one to two bushels of shells could probably be successfully employed in most ponds. In others, however, where setting at the bottom will not take place because of unfavorable conditions, or because the enemies there are too numerous, other methods, such as use of rafts or floats supporting large quantities of cultch near the surface, as practiced by Japanese oyster culturists, could be advantageously employed.

In ponds having a channel connecting with the outside, the rafts carrying the cultch should be kept in a pond only long enough for the cultch to secure a sufficient number of spat. Under favorable conditions, this could be a matter of only a few hours. After that the rafts should be towed outside where the recently secured set can be planted, and the rafts, reloaded with cultch, returned to the ponds to obtain more set. By using this method, a large quantity of set may be procured from relatively small ponds in which a heavy setting continues throughout a long period.

III. For planting shells and for using other seed collectors at the most advantageous time, the following information would be desirable:

a. Time of gametogenesis and beginning of spawning of oysters.
b. Relative intensity of spawning during different periods of the summer.
c. Rate of growth of larvae, length of larval period, and rate of survival of larvae to the setting stage. Staining larvae with vital dyes may help solve this problem (Loosanoff and Davis 1947).
d. Beginning, extent, and end of the setting period.
e. Daily intensity of setting in different areas of the pond.
f. Intensity of setting in relation to depth. This may be determined by using simple vertical collectors, which have proved adequate for such studies (Loosanoff and Engle 1940).

In shallow, warm ponds where the majority of adult oysters will discharge their spawn early in the summer, it may be advantageous, after the first wave of setting, to introduce another supply of ripe but unspawned oysters. Spawning of these oysters could be purposely delayed by keeping them in water of such low temperature that they could not discharge their sex products (Loosanoff and Davis 1951). By using this method, heavy spawnings in the pond could be induced at desired intervals throughout the summer.

IV. Observations should be made to determine the following:

a. Rates of growth and survival of spat on different beds of the pond from the beginning of setting to the beginning of hibernation.
b. Percent of survival of the set, if it is left in the pond throughout the winter. In some shallow ponds that freeze solid, the set may have to be removed to other grounds before the onset of winter.
c. Whether introduced spawners, if such are used, survive winters well and are able to develop spawn the following year. Compare their behavior and condition with those of native stock.

Selection of desirable races may be an important aspect in pond culture because many strains of oysters transplanted from one district to another do very poorly in new surroundings (Loosanoff and Nomejko 1951). Hence, it may be necessary, in some instances, to develop a sufficiently large stock of spawners from the pond population to assure enough set that will grow well under local conditions. On the other hand, some ponds may be populated with oysters which do well in these ponds, but which, upon transplanting to growing grounds in open waters where conditions are different, show unusually high mortality or poor growth. Obviously, such races are undesirable as spawn producers if the resulting set is not to be used locally. They should be removed or destroyed, and the ponds repopulated with a race that is known to do well in the area to which the set is to be transplanted. We can suggest two methods for destroying undesirable populations—first, lower the salinity in the pond for periods long enough to kill all the oysters, and second, use specific poisons.

If it is necessary to bring outside spawners into the ponds, it should be done early in the season, before the drills begin to deposit egg-cases. This will prevent carrying the egg-cases, together with the spawners, to the new locations. In some instances, it may be practical to obtain spawners from relatively brackish areas. Since these oysters will not be infested with starfish, drills, or sponge, they will not carry along these enemies.

The relative ease with which the ponds could be stocked with desirable strains of spawners suggests the possibility of developing races that have the qualities considered important in oysters. For example, in our waters it takes from four to six years to grow an oyster to marketable size. However, because of the recent advances in the cultivation of lamellibranch larvae, we can now try to breed out a race of fast-growing oysters which will reach marketable size in less than half that time. This desirable quality could be combined with others of equal importance, such as development of unusually large meats containing much glycogen. Obviously, if such races could be developed in the laboratory to be later used as spawners under natural conditions, the entire aspect of the northern oyster industry would become radically changed.

In conclusion, a few words should be said about fertilization of the ponds to offer more food to oyster larvae, spat, or adult oysters. This measure, which is so widely used in fresh water fish ponds (Neess 1949; Mortimer and Hickling 1954), has been considered, naturally, as one of the steps that will eventually assure success in the pond culture of oysters. Unfortunately, even now, sufficient information is not available as to the food requirements of oyster larvae or adults. We have learned, nevertheless, from recent experiments (Davis 1953) that oyster larvae are very selective in their food, and that usable food organisms are ordinarily not too numerous in the blooms which follow the addition of common fertilizers to sea water.

We have also found that green algae, such as Chlorella, which multiply rapidly after the addition of fertilizers, are not utilized at all by oyster larvae during their early stages of development (Davis 1950), and that heavy concentrations of Chlorella cells and their external metabolites will kill bivalve larvae (Loosanoff 1954b). Furthermore, it has been demonstrated that even adult oysters can feed efficiently only in relatively clear water, and that if the micro-organisms exceed certain numbers, they interfere with the feeding of the oysters and may eventually even kill them (Loosanoff and Engle 1947). Considering these dangerous aspects of fertilization, and also our exceedingly limited knowledge of food requirements of oyster larvae and adults, it may be advisable to proceed cautiously in fertilizing the ponds until more is known about this matter.

At present, we are principally interested in pond cultivation of the American oyster, *C. virginica.* Nevertheless, we think that similar approaches, with proper modifications, can be used for cultivation of other molluscs, such as clams, especially *Venus mercenaria*, and, perhaps, even scallops.

Consideration should also be given to the possibility of utilizing ponds for cultivation of the European oyster, *Ostrea edulis.* These oysters, which have been successfully grown in ponds and claires in Europe for some time (Orton 1937), were brought here from Holland in 1949 and planted in the waters of Connecticut and Maine (Loosanoff 1955). Because they survived, grew well, and propagated normally in their new environments, they should do well in many of our ponds.

This paper is largely based upon the outline which I prepared in March 1953, and later sent to my colleagues on the Atlantic and Pacific Coasts for criticism and suggestions. May I now offer my thanks to those who commented on it.

SUMMARY

The article proposes the approaches for ascertaining the suitability of small, enclosed or semi-enclosed salt water bodies for the propagation of oysters and other molluscs. It suggests the steps to be taken in studying the physiological, chemical and biological characteristics of such ponds, and recommends certain devices and methods that should improve their conditions.

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SOME RELATIONS OF FAUNAL DISTRIBUTIONS TO SALINITY IN ESTUARINE WATERS

From September 1951 to June 1953 the writer carried on a study of the lower Mermentau River basin in southwest Louisiana for the Corps of Engineers, U. S. Army (Gunter 1954). The aim of this work was to obtain information on the biological effect of water level controls in the two large brackish lakes and the surrounding marsh. The project was related to wildlife management and the full results will be published elsewhere (Gunter and Shell, *in press*). However, certain data collected in this connection are worth special emphasis quite removed from marsh and fishery management.

Grand Lake and White Lake lie in the marsh in the lower Mermentau River basin. The river runs through the first, which is also connected by a narrow channel to White Lake, which in turn is connected to Vermilion Bay. The area of these two lakes is 180 square miles. They are weakly saline and are not given to rapid salinity changes. In fact, they are probably as stable bodies of low salinity water as can be found on the Gulf coast.

Bays and estuarine waters act as nursery grounds for large numbers of marine species (Gunter 1945, 1950; Reid 1955). They harbor many species which live in purely marine waters as adults. Many of the marine specimens caught in the course of the work were less than an inch long (Gunter and Shell, *op. cit.*). Probably the young of shallow water marine animals withstand low salinities better than their elders. At least the young are found more often in such waters.

Field Observations

It has been shown (Gunter 1955) that three localities in Texas waters with average salinities of 19.0, 19.8 and 22.1 per mille over an eight month period, showed a difference in oyster condition and differences in both sessile and motile associates. Stations with differences of 3 or 4 parts per thousand salinity showed great variations in abundance of the same organism. It was suggested that small salinity differences "may exert more influence than is realized or expected."

In the Mermentau work trawl and seine stations were set up in Grand and White lakes and in Little Bay, a small arm of Vermilion Bay. The numbers and species of animals caught in the three water bodies during six rounds of these stations, over the period from September 1951 to June 1953, have been presented elsewhere (Gunter and Shell, *op. cit.*) and will not be repeated here. Thirty-five species of animals were caught, two mollusks, five crustaceans and twenty-eight fishes. Table I shows the species caught more than fifty times in the whole area. Table II is a summary. The salinity readings cover a twenty-two month period.

The number and numbers of species of fresh water animals decreased markedly from Grand Lake through White Lake to Little Bay, although the average salinity differences were small. The number of marine animals did not differ greatly in White and Grand Lakes, but was considerably greater in the bay, although there was one less trawl haul here. The average salinity in the lakes was 0.97 as compared to 1.44 per mille for the bay, a difference of less than 0.5 parts per thousand. Such differences seem to be important over large and stable estuarine areas.

Table I. The most numerous species and the number caught, September, 1951-June, 1953 at all stations

Common name	Species name	Number caught
Menhaden	Brevoortia sp.	2,230
Bay anchovy	Anchoa mitchilli	941
Croaker	Micropogon undulatus	900
White shrimp	Penaeus setiferus	566
Broad sole	Trinectes maculatus	267
Rangia clam	Rangia cuneata	213
Silverside	Menidia beryllina	171
Grass shrimp	Palaemonetes sp.	152
Blue crab	Callinectes sapidus	121
Fresh water catfish	Ictalurus furcatus	112
River shrimp	Macrobrachium ohione	80
White trout	Cynoscion arenarius	70
Gulf gizzard shad	Signalosa petenense	68
Brown shrimp	Penaeus aztecus	61
	Totals........	5,952

Table II. A summary of salinities in parts per thousand and the numbers of species and specimens caught in Grand and White Lakes and Little Bay

	Grand Lake	White Lake	Little Bay
Trawl stations..........	2	2	1
Seine stations..........	1	1	1
Salinity range..........	0.08-2.70	0.11-2.70	0.16-4.05
Salinity average........	0.65	1.16	1.44
Fresh water species.....	10	6	5
Marine species..........	17	18	19
Fresh water specimens...	124	80	50
Marine specimens.......	1,771	1,647	2,457

The Predominance of Marine Animals in Low Salinity Waters

Pearse (1936, 1950) and Gunter (1942, 1945, 1950) have noted that the fauna of brackish water is marine. This holds true even in the very lowest salinities. The tables presented here show that both in species and numbers of specimens the marine species predominate, and in the number of specimens the predominance is overwhelming. Even if such estuarine species as *Rangia cuneata* are excluded from the marine group, the general picture is not changed.

Not only is the fauna of estuaries marine but a good many more marine fishes, about nine or ten to one, invade fresh water than come from fresh water into sea water (Gunter 1942). The last statement applies to movements of individual fishes. Kilby (1955), however, as a result of his work on the fishes in low-salinity marsh areas in Florida says the population is dominated by fishes with freshwater affinities. This arises because he classed with freshwater species some fishes of the family Cyprinodontidae, although the species themselves are marine to all intents and purposes. For instance, three cyprinodontids, *Fundulus grandis, F. similis* and *Cyprinodon variegatus* were included with what he calls the freshwater-brackish group. These fishes are euryhaline, but they live and breed in salt water and they can withstand very high salinities. They are indubitably marine. I have taken the last in the Laguna Madre of Texas at a salinity of 71.5 per mille, over twice that of sea water (Gunter 1945), and a former student, Mr. Don G. Simpson, took this fish in a tide pool which was over 140 parts per thousand salt.

A second group listed by Kilby in the same category lives in brackish water. It includes *Adinia xenica, Lucania parva* and *Mollienisia latipinna,* all cyprinodontids. They can live in fresh water but they are brackish water fishes and Herre (1929) has reported the last species from water with a salinity of 85.0 per mille. They are not so well adapted to salt water as the first group, however, and probably should not be included in either the freshwater or salt water groups, although in habitat at least they belong more in the latter. They may be called brackish water species. Kilby's figures show that, according to the above classification, he caught 7,025 marine fishes, 9,435 brackish water fishes and 4,883 freshwater fishes in the marshy area with a salinity ranging from 1 to 25 per mille, where 52 percent of the readings were from 4 to 7 per mille. His collections were made with short seines.

In ranking fish species as freshwater or marine we must go by present habitats rather than family affinities, or we would soon arrive at some weird groupings with regard to such things as the freshwater atherinids and the marine catfishes, as well as others that could be mentioned. Conclusions based on such groupings would go similarly astray.

The statement that the fauna of low-salinity estuarine waters is marine applies to the invertebrates as well as the fishes. If one group of fishes, the cyprinodontids, were removed from consideration, no question about the matter would have arisen. The question of whether more freshwater families of fishes have representatives moving from fresh water into the sea than there are marine families moving into fresh water has not been critically examined, but it is certainly true that one vigorous group of freshwater fishes, the Cyprinodontes, has moved down to the margin of the seas and some of the species are now marine.

It should also be remembered that these fishes seem to be held very close to shore by the need for cover (Gunter 1945) and are not limited by salinity. A similar situation holds true with some shrimp of the genus *Palaemonetes* of the freshwater family Palaemonidae. Therefore, collections made by short seines close to shore give an entirely different picture from those made only a few feet farther out by trawls or other gear. The presence of cyprinodontids and palaemonids near shore has been clearly demonstrated by the writer (Gunter 1945, 1950) in tables comparing shore and offshore fauna of the bays. Simpson and Gunter (*in press*) have shown that the salt water Cyprinodontes are primarily fishes of shore ponds and inlets rather than bay shores. Collections in open waters of all estuarine areas show an overwhelming predominance of marine species, without the presence of marine or brackish water species that were derived from freshwater families. Since the marginal or shore areas are small compared to the area of well populated open waters, the general statement that in numbers the fauna of estuarine waters is predominantly marine would hold true even if the hordes of cyprinodontids and palaemonids next to shore in some waters were classed as freshwater animals without equivocation.

One striking peculiarity of the Louisiana marsh area is the virtual absence of cyprinodontid fishes over the general expanse.

H. T. Odum (1953) has given an analysis of the invasions of marine animals into the fresh waters of Florida and has shown that the chloride contents of these waters over much of the peninsula are relatively high. He divides the salinity range of estuarine waters in parts per million chloride into four cycles: 1.9-19, 19-190, 190-1,900 and 1,900-19,000. The first division is partly within the chloride range of rain water. The equivalent salinities in parts per thousand of the other three divisions are: .034-0.346, 0.346-3.46, 3.46-34.3. He adds that the intermediate zones are not present in most estuaries, but that where all zones are present it is not correct to say that marine components dominate them. However, there are some stable areas of a few hundred square miles equivalent to Odum's third zone and a large part of his second. White and Grand lakes are examples. He says that freshwater organisms predominate in the first two cycles, fresh water and marine organisms share the third and marine organisms only dominate in the fourth. However, the actual division of dominance of marine organisms over fresh water species lies somewhere in Odum's second cycle. In May and August, 1952 and January and June, 1953 Gunter and Shell (*op. cit.*) made seventeen stations where the salinities ranged from 0.08 to 0.26 per mille, by titration. Eleven freshwater species and 148 specimens were caught; thirteen marine species and 679 specimens were taken. At three stations with salinities of 0.08 per mille there were four fresh water species and 65 specimens, and eleven marine species comprising 165 specimens. It is such hauls as these which led to the conclusion that estuarine fauna is predominantly marine even at the lowest salinities. Statements to the contrary do not coincide with the evidence.

DISCUSSION

Redeke (1932) came to the conclusion that the chloride content of the water was the most important factor governing the distribution of estuarine species, a view which has been questioned by other workers. The works of Segerstråle (1951, 1953) and Kilby (1955) agree with Redeke's conclusions. The observations recorded here also tend to confirm his views. Catches at individual stations showed that certain animals drop out of the picture at certain low salinities, but are found again in the same area when the salinities rise. Furthermore, the effect of lowering salinity is seen in the decline in numbers of a species. For instance, only two white shrimp, *Penaeus setiferus,* were taken at a salinity of 0.44, but over two hundred were taken at about 0.80. Several other species showed the same thing, as demonstrated in Table III. This table shows that the numbers of various animals declined sharply a certain low salinities. It appears that the sensitivity of estuarine animals to salinity has a great deal to do with their distribution.

TABLE III. The salinity ranges per mille at which the four most abundant fishes and the three important crustaceans were taken are shown, with the numbers caught. Sharp declines at certain lower salinity limits are evident. Similar tables for the other species may be derived from data presented by Gunter and Shell (*in press*)

	Salinity Ranges	Numbers Caught	Number of Hauls	Average per haul
Brevoortia	0.18-0.29	10	8	1.3
	0.41-0.93	1,038	15	69.2
	1.14-2.70	1,175	13	90.4
Anchoa mitchilli	0.08	1	3	0.3
	0.10-0.19	283	12	23.6
	0.21-0.93	464	20	23.2
Micropogon undulatus	0.08	2	3	0.7
	0.10-0.93	423	30	14.1
	1.84-4.05	430	12	35.8
Trinectes maculatus	0.08	2	3	0.7
	0.10-0.93	185	30	6.2
	1.84-4.05	64	12	5.3
Callinectes sapidus	0.10-0 73	33	24	1.3
	0.75-0.82	28	4	7.0
	1.14-4.05	58	14	4.1
Penaeus setiferus	0.44	2	6 (0.41-0.47)	0.3
	0.78-0.82	238	5 (0.73-0.82)	47.6
	1.84-4.05	326	12	27.2
Penaeus aztecus	0.78-0.82	9	2	4.5
	2.16-2.70	48	7	6.9

The low-salinity limits for estuarine animals cannot be stated sharply. Oyster mortality at low salinities depends on the temperature of the water, the rate at which the salinity drops, the length of time it stays low, the fatness of the oysters and the previous salinity at which the oysters were living (Gunter 1953). Salinity limits may also depend somewhat on the size of the animal. The lower limits an animal will "tolerate" are doubtless more complicated than the mortality limits, for we do not know when an animal feels ill at ease or even what toleration means precisely in physiological terms. We do know, however, that animals distribute themselves over definite salinity ranges and seem to be quite sensitive to salinity differences near the lower side of these ranges. Under normal conditions the upper salinity limits are seldom exceeded in nature, for as I have pointed out before (Gunter 1945, 1950) nearly all estuarine animals, except a few transients from fresh water, can tolerate full sea water.

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REVIEWS

SCHRÖDINGER'S SOURCES OF SCIENCE[1]

Ernst Mach, the famed physicist, once referred to the "scarce and poor remnants of ancient science," and continued: "Our culture has gradually acquired full independence, soaring far above that of antiquity. It is following an entirely *new* trend . . . The traces of ancient ideas, still lingering . . . constitute impediments rather than assets." Possibly many of us do hold this and similar opinions, and consider that the philosophies of classical antiquity are something for the birds, at least not for modern scientists.

Dr. Schrödinger, internationally famous for his work on wave mechanics in the field of quantum theory, and author of several successful books for the general reader, refers to this idea as "supercilious crudeness." In a volume the smallness of which thoroughly belies the revolutionary message it develops, the author, acknowledging his indebtedness to Theodor Gomperz and John Burnet, traces the origins of our scientific thinking back to the surviving fragments of Greek philosophers.

Although this book was written for all scientists, it is the reviewer's opinion that it holds a very special value for ecologists, and is the finest short treatise of its kind for the younger generation entering the field. Even more than other biological sciences, ecology, usually tracing its history only to Warming and Schimper, is destitute of the rich traditions that have accumulated in other fields. Although a knowledge of those traditions will not change our observational and instrumental data, it will greatly alter our appreciation of those data, and their organization into a mature science.

In the introductory chapter, the author discusses the nature of, and present-day antagonisms among, science, religion, and philosophy. Then he draws us back twenty centuries to antiquity, when these outlooks upon the world were intertwined and combined without distinction. Moving forward again to this century, it becomes understandable that much of our present scientific way-of-thinking is a direct and unacknowledged inheritance. It is an inheritance effected by the coincidence of our being a part of Western Culture (and not of the Orient). It was able to continue because the ideas were congenial to our psychological make-up. (What we think, seems "natural.") It represents, however, but one arbitrarily isolated facet of the welter of Greek thought. This approach would be but an exercise in history *but for the fact that* contemporary science has met some critical impasses, to which this history is the key. "Pre-conceived ideas and unwarranted assumptions may have been taken over by the fathers of modern science, and would, by their authority soon be perpetuated. Had the highly flexible and open-minded spirit that pervaded antiquity continued, such points would have continued to be debated and could have been corrected. A prejudice is more easily detected in the primitive, ingenuous form in which it first arises than as the sophisticated ossified dogma, it is apt to become later. Science does appear to be baffled by ingrained habits of thought, some of which seem to be very difficult to find out"; and ecology has its share.

Dr. Schrödinger eclectically picks and chooses, without regard to Greek chronology, but with clear reference to ingrained habits of contemporary thought. It is these habits that are dangerous because we are as unconscious of them as we are of atmospheric pressure. In the second chapter the bifurcation of world interpretations, subjective "pure reason" on one side, and the material senses on the other, are traced to Parmenides and Protagoras respectively. Parmenides' purity of course has been in disfavor through the recent decades of "objective," sense-derived, experimental science. Yet "pure reason" is always ready to enter, either as subtle intrusions from what is now metaphysics and religion, or else in the guise of science itself, as evidenced by some of the views of Clements. To confuse the matter even further, today some of the proudest prophets of Protagoras, priding themselves on their objectivity (that is, pure sensualism), are smug in their supposed monopoly of what *they* call "reason." In the enlarged perspective of two millenia, this use of the word reason is as confusing to us as is Communist use of the word "democratic."

The third chapter is devoted to the Pythagoreans, with their enormous emphasis on numbers and mathematics, "bordering on religious prejudice." "The basic doctrine . . . was that *things are numbers.*" Without once belittling the importance of the resulting mathematical research, "is it very irreverent to remember . . . that we were recently told by an eminent scientist that the total number of elementary particles in the world was 16 x 17 x 2^{256}, where 256 is the square of the square of the square of 2?" And I myself always remember that long strange night I once spent with two statisticians, until New York bar-closing time, discussing the world in their terms. Biotic communities were not exempt from the inclusiveness of their zeal and fervor.

The Milesian School (Thales, Anaximander and Anaximenes) as discussed in the fourth chapter is the most direct single source of our natural sciences. Xenophanes and Heraclitus, two independent and unrelated thinkers, are given their share of praise in the following chapter. Then comes a section on the "atomists" Leucippus and Democritus. Let us not too hastily relegate atomism to the chemists and physicists. We ourselves never tire of defining the "association" and the "fundamental unit," even though each definition is elusively elastic to everyone except its ecologic Maker. Once a definition however is accepted by a group, exercise of it can become almost an obsession, as evidenced by the -etumitis of Montpellier. Since for each action, nature decrees a reaction, we should not overlook the Wisconsin continuum, a philosophy that could become extremist, and one that arose in conscious opposition to the phytosociological atomists.

The concluding chapter is a recapitulation of the main points. So effectively however has the book been written that, to me, it was an anticlimax. That *nature can be understood* is the fundamental assumption of contemporary science, and the author has conclusively shown that the roots of our thinking on this subject lie in Greek knowledge. An awareness of these various roots, it seems to the reviewer, is essential in our own field of ecology if controversies are to be welcomed and evaluated with proper perspective. In this manner data and their interpretations can eventually be amalgamated into a living and growing science which is not forgetful of the arbitrariness of its philosophical foundations.

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[1] Schrödinger, Erwin. 1954. Nature and the Greeks. Cambridge and New York: Cambridge University Press. 97 pp. $2.00.

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Some Recent Contributions to Marine Ecology

Three books have recently been published which review certain aspects of marine ecology. Taken together they summarize current knowledge and interpretations of littoral communities, the physical nature of the ocean bottom, and animal life of deep ocean waters. Two of the three are based upon lectures delivered in the United States.

THE LIFE IN THE SEA by Ralph Buchsbaum[1] is based upon the 1954 Condon Lectures of the Oregon State System of Higher Education given in Eugene, Corvallis, and Portland. The stated purpose of these lectures is "To interpret the results of significant scientific research to the non-specialist," and this is what Dr. Buchsbaum has done by way of an "introduction to the study of the myriad life of the sea and its ecology." It is a non-technical discussion of a semi-popular nature which reviews highlights of marine ecology. It is slanted toward the Pacific Coast of North America for the local interests of his audience. While there are no new facts or interpretations presented, the booklet is an interesting introduction to the subject for students or for ecologists who have themselves not worked in the field of marine life. It begins with a historical sketch of the exploration of the sea and study of marine life from the oldest records to the present day. This historical account occupies more than a third of the text. Attention is also given to current research by oceanographic laboratories in various parts of the world. Marine communities are described in general terms; and certain principles involved in zonation, distribution, abundance, and food chains are explained. The discussion is based largely upon the well known work of the Stephensons. Rocky shores, sandy beaches, and muddy shores are briefly described. The booklet ends with an indication of "some current problems in oceanography." A few selected references, most of which are of a general nature for reference reading, are listed. It is profusely illustrated with excellent pictures, seventy of which are half tones, and the greater number of these are original. Fortunately, the many typographical errors in the List of Illustrations are not repeated in the text or in the legends.

THE OCEAN FLOOR by Hans Pettersson[2] is similarly an illustrated review essay based upon a lecture. This was the Silliman Memorial Lecture at Yale University for 1952. Like the preceding publication, this is largely historical in approach and is a summary-review in non-technical language of highlights in past and present interpretations of the physical nature and structure of the ocean bottom. It is international in scope, including work of scientists of all nations which have been active in physical oceanography. While most attention is given to marine geology, it has ecological interest because of the relation of ocean sediments to life in the sea. There is also a chapter on the "Bottom Waters of the Ocean and Their Movements" and of "Life in Great Depths." Dr. Pettersson has incorporated his own recent work with his account of the work of others from the very beginning of research on the ocean floor to the present day. He gives his own latest interpretations although the supporting data will be presented elsewhere. He points up the questions now in the minds of physical oceanographers and indicates those problems which are promising for investigation. Special reference is made to the contributions of the *Albatross* expedition sponsored by the Swedish Oceanographic Institute of which Dr. Pettersson is the director. Latest measurements on sedimentation obtained from that expedition are included. The theory of continental drift which is of interest to some ecologists is found not tenable in light of recent knowledge of the ocean bottom. A number of controversial matters are discussed, particularly the role of turbidity currents in sculpturing the ocean floor. It is concluded that they play no dominant part. The discussion is thoroughly documented with notes, and there is a general index.

The third contribution concerns ASPECTS OF DEEP SEA BIOLOGY by N. B. Marshall.[3] This is a review of present knowledge about deep sea organisms and their ecology. This book also has a historical approach to the subject and is essentially a summary of research since the beginning of deep sea studies initiated by the *Challenger* Expedition of 1872-76. Modern methods of oceanographic research are discussed. Along with descriptions of deep sea organisms and their adaptations, movements, behavior, food habits, and life histories, there is a discussion of ecological principles. For the most part this is elementary in nature, but it is needed for the general reader. Theories as well as facts are considered in describing marine environments, populations, communities, and their interrelationships. The approach is ecological throughout. The bulk of the text consists of selected accounts from recent publications in the field, and these are well documented. A small amount of unpublished work accomplished by the author is incorporated. An outstanding feature of this book is its treatment of the color and color relations of deep sea animals illustrated with five color plates produced by the author's wife, Olga Marshall. Other highlights are chapters on deep sea food chains, vertical patterns of distribution, sense organs, sound and light production, and life histories. There are references at the end of each chapter, all of which are quoted in the text, and there is an index-glossary at the end. Most of the black and white illustrations, also prepared by Olga Marshall, are taken from published sources. The text seems to be quite free from error although unfortunately Claude Zobell is referred to as Clifford Zobell. Many challenging questions are raised, most of which cannot be answered with our very limited knowledge of the deep sea.

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[1] Buchsbaum, Ralph. 1955. The life in the sea. Eugene, Ore.: University of Oregon Press. x + 101 pp., 9 figs., 35 plates. $1.50.

[2] Pettersson, Hans. 1954. The ocean floor. New Haven: Yale University Press. xv + 181 pp., 48 figs. $3.00.

[3] Marshall, N. B. 1954. Aspects of deep sea biology. New York: Philosophical Library. 380 pp., numerous black and white figs., 5 color plates. $10.00.

The chief contribution of these three works is the presentation of a modern review and synthesis of published literature on littoral marine ecology, dynamics of the ocean bottom, and deep sea biology. While little if anything new is presented, they are well-written summaries for the student and non-specialist. All of them are historical in approach, and all of them point the way toward problems awaiting solutions.

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INLAND WATERS IN NATURE AND CULTURE[1]

August Thienemann, Director of the Hydrobiologischen Anstalt der Max Planck-Gesellschaft zu Plön, has had many years of personal experience with the limnology of the waters of Germany, and his small book is an effective presentation of some of the important conclusions to which his observations have led him. In addition, a year spent in limnological study in the East Indies allows him to make some very interesting and instructive comparisons between production in tropical waters and that in the temperate waters of the latitude of Germany. The book is obviously not directed particularly towards the specialist in limnology, though there is no question that many such specialists would greatly broaden their outlook in their chosen field were they to master the concepts Thienemann has postulated. Biology students would find much of value, either as a general exposition of the close correlation between theoretical and applied biology, or as a survey preparatory to a more detailed and thorough study of the broad field of limnology, and the same may be said for the intelligent layman, who is the primary target of the publication.

Thienemann divides his book into four main sections. In the first section he surveys some of the major plant and animal forms and describes some of their adaptations to their special ecological niches in the water. He emphasizes, however, that limnology is not merely the study of life *in* the water, but is primarily the study of the life *of* the waters—i.e., it is an ecological study. Every organism not only depends upon the environmental factors in the water for its existence, but in turn it alters the water in which it lives, through its life activities.

The second section compares (in certain generalities) the limnology of streams and of lakes. The major differences, such as temperature, light, chemical characteristics, currents, influence of the surrounding land, and influence of form are stressed, but at the same time the author points out that the river influences the lake, and the lake influences its outlet streams. The lake can be spoken of as a "microcosm," though only with the understanding that it is not strictly so, for many allochthonous influences come to bear upon it. The stream can never be thought of as a microcosm, because its intimate relationship with the surrounding land makes the allochthonous influences predominant.

Section three is a discussion of production and of lake types. The measurement of production, of course, is one of the most difficult problems in limnology, and Thienemann very commendably considers the ramifying complications of the subject without hopelessly losing the reader in the maze. Basic production (by green benthic plants and the phytoplankton) in itself is sufficiently difficult to measure quantitatively, and the complications involved in the dynamics of the food chain have led the author to believe that the total production, in all of its ramifications, can never be measured quantitatively.

The final section, entitled "Water—The Sorrow of Europe," is a consideration of applied limnology. Fresh water as a source of food and of materials for mankind is briefly discussed, then considerable space is devoted to the dwindling water supplies occurring in Germany (and in all industrialized lands) in the face of mounting demands for good water, and to the domestic and industrial pollution of natural waters. Throughout this portion of the book Thienemann emphasizes over and over three things: 1) the need to reverse the trend towards the indiscriminate drainage of swamps, lowering of lake levels, and straightening of streams to speed the run-off of water, 2) the need to prevent the uncontrolled pollution of natural waters by industries and municipalities (in an industrial state, if one only knew the history of that which is put before him as drinking water, one would never drink water again!), and 3) the necessity of having trained limnologists as consultants in all state and industrial activities having to do with the use or management of water supplies, be they surface or subsurface supplies. Polluted rivers and lakes are spoken of as "cloacas," and the author regretfully speaks of the beloved Rhein as *"der Pissrinne Europas."* The whole question of applied limnology is approached from the point of view of ecology: man is, more than many other animals, dependent upon natural waters as a source of food, transportation, recreation, industry, etc., yet in his activities he modifies his aquatic environment enormously. This has been increasingly true since the rise of modern industry. The author makes it clear, however, that he prefers to think of the effects of modern man upon natural waters as the result of civilization, and not of culture *"denn was da geschieht, ist 'Unkultur.'"*

Die Binnengewässer in Natur und Kultur is one of a long series of volumes devoted to making scientific subjects clear to the general public, and there are a number of similar series appearing throughout Europe. It makes us wish, in this country of comic books, murder mysteries and "science" fiction, that our own public might have more benefit from small, authoritative books on the many aspects of science, written by those most actively aware of, and engaged in, fundamental research. That such books do not need to "write down to" the public, nor to be "over their heads," is shown by Thienemann's very commendable effort.

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[1] Thienemann, A. 1955. Die Binnengewässer in Natur und Kultur. (Verständliche Wissenschaft, Bd. 55) Berlin: Springer-Verlag. viii + 156 pp., 50 fig. 7.80 DM., $1.85.

EXPERIMENTAL SOCIOLOGY OF HIGHER PLANTS[1]

Frequently a science is assumed to have matured if it has progressively evolved through an observational stage to an experimental stage. At intervals in the succession theory has entered, to be tested both by observation and experiment. By these criteria Professor Knapp's book marks the coming of age of plant sociology as a science.

Knapp takes for granted that plant communities exist; that of all single criteria a floristic list best defines a vegetation stand, including its habitat; that inductively, by objective comparison of such lists, a concept of the plant community can be reached; and that the causes of community organization can be approached through experimental studies of habitat requirements as modified by competition with other plants of the local flora. Knapp, then, relates experimental ecology to defined, named, and thoroughly described plant communities.

Considering problems and goals, an *experimental* plant sociology has certain logical advantages in providing explanations of community occurrence and structure. These advantages include the ready use of induction. Observation lacks the theoretical background necessary to set up models which can be tested statistically by observed data. The simplifications of experiment are therefore necessary. A fundamental logical defect in habitat analyses—that they cannot demonstrate causation, but only coincidence—is pointed out.

Under "The most important possibilities of an effect of higher plants on one another, alterations of environment under the influence of neighboring plants" is treated in what we in the U. S. ordinarily call "vegetation influences," changes in the immediate climatic and edaphic factors brought about by vegetation itself. Many American data are from forestry and have been summarized by Professor Kittredge in his book *Forest Influences* (1948). Of Knapp's literature references in this section, 24 were published later than Kittredge's book, 41 are not included by Kittredge, and 3 are common to both books. This certainly is no disparagement of *Forest Influences*, which is most valuable and unique in its field—as the Russians partially demonstrated by translating it in 1951. It does show, however, that even in his small section on vegetation influences, Knapp contributes both new data and new ideas to American ecology

Besides these modifications of climatic and edaphic factors, Knapp also considers the effects of secretions from living plants, materials derived from litter, and modifications by microorganisms and animals.

In the next section of 32 pages, data on the sociology of seed germination are given. The influence on germination of different soils, temperatures, various numbers of seeds of the same and different species, established stands of the same plant as that being germinated and established vegetation of different kinds of plants, litter, and relationships to plant succession are all reported for a considerable number of species. Standard errors of mean germination percentages are given throughout, so that significance of results can be readily assessed.

Then Knapp considers the sociology of mature vegetation stands. Pure stands are first treated (31 pages), then those composed of many species (81 pages). In pure stands, of course, beyond a certain density, size of plant would be expected to decrease with increasing numbers of plants per unit area planted. Knapp presents data on this point, as well as the relation of such a curve to the ontogenetic development of the plants and to their possible favorable or unfavorable influences on each other by root excretions, etc. The curves found are a function of type of plant and type of site. Data from normal stocking of various forest site classes clearly illustrate the last point. Obviously, weight, height, and seed production are all affected by plant density, and Knapp has compiled or produced data on each. In addition there are some data on measurable changes in environment brought about by differences in plant density. These include shade and root competition, resulting in suppression which only some species can endure, and toxic secretions, so well known now from Bonner and his colleagues' work on guayule (*Parthenium argentatum*), among other plants.

In vegetation, composed of many species in numerous —but evidently not infinitely numerous—mixtures, different plants come to dominate others in special ways—by more rapid growth above and below ground, root interactions, and toxic secretions affecting other plants. Plummer's and Robertson's work[2] is omitted under the first point, but then it is true that few plant sociological data have been forthcoming to utilize the autecological data produced in connection with western rangeland reseeding. On the last point Knapp includes much material published since Bonner's review[3] and some significant items published before. It is interesting that much of the later work, done from a strong phytosociological slant, has given point to biochemical data which, outside the conceptual framework of even such a young and almost primitively developed science as plant sociology, are actually ecologically misleading.

Three more sections make up this last half of the book devoted to the experimental plant sociology of vegetation itself. The success of plant species in vegetation as influenced by internal and external factors includes a valuable section on genotypes, including ecotypes. Species' success is also shown to be influenced by stand density, nutrient supply, water, light, soil pore space, grazing, and parasites. The grazing section is weakest from an American standpoint, omitting most of the U. S. data from experiments designed to show effects of different grazing regimes on plants of various types of western rangelands. Its conclusions from meadows and pastures, however, largely parallel ours. Knapp's omissions can be rationalized on the basis that most of our western rangelands are poorly characterized from a plant sociological standpoint, and that the plant sociology and experimental treatment of range vegetation have been uncorrelated.

The third section considers "Effects of communities on the individual plants and the species." Changes are brought about in the genotype by selection, as exemplified by flax weeds. Various plant genotypes are intimately associated, for one reason or another, with particular associations of plants. Also, of course, the external form of a plant is altered according to the community it inhabits. Changes in flower and fruit development, alkaloid content, yield, and height result. Next, Ellenberg's[4] differentiation between physiological and ecological tolerance is considered. A species will grow artificially in pure culture in a quite different range of environment from that under which it is found naturally when competing with other plants. Of course, tolerance is not a linear function, but has minimum, optimum, and maximum points. Knapp points out that the physiological and ecological optima need not even coincide. As an extreme case, two separated ecological optima may result if a eurytopic species is not able to compete with other plants in the center of its tolerance range.

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[1] Knapp, Rüdiger. 1954. Experimentelle Soziologie der höheren Pflanzen. Stuttgart: Eugen Ulmer. 202 pp. DM 14.50, $3.45.

[2] Plummer, A. P. 1943. The germination and early seedling development of 12 range grasses. Amer. Soc. Agron. Jour. 35: 19-34.

Robertson, J. H. 1943. Seasonal root development of sagebrush (*Artemisia tridentata*) in relation to range range reseeding. Ecology 24: 125-126.

[3] Bonner, J. 1950. The role of toxic substances in the interactions of higher plants. Bot. Rev. 16: 50-65.

The last major section of the book treats the performance and change of plant communities. Production per unit area is definitely a function of species composition within one otherwise uniform ecosystem. Seedlings of any given species show quite different survival and growth in different communities. Here are data which could make "natural selection" a quantitative and, therefore, more exact study. These data also help to explain the entities of associated species we frequently find expressed in vegetation as recognizable communities, rather than vegetation representing one continuum. If one species of a characteristic species combination is omitted, interesting changes in relative amounts of the other species result. The last topic concerns experimental plant succession. The promised second volume is to contain more on this subject and on methods.

Knapp's little book is obviously not a handbook. However, the literature in most areas seems well-treated, and always interesting ideas are suggested, illustrated by Knapp's and his colleagues' data plus those from the literature. The actual number of references is large, well-chosen, and well-distributed geographically, with no evident local or language biases. The number of references compares with those cited by Daubenmire and Braun-Blanquet in their texts. Not the least virtue of Knapp's book is the treatment of well-known data in a new and novel light—from the veiwpoint of experimental plant sociology.

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[4] Ellenberg, H. 1953. Physiologisches und ökologisches Verhalten derselben Pflanzenarten. Ber. deutsche Bot. Ges. **65**: 350-361.

TWO INTRODUCTIONS TO CONSERVATION[1]

There must be an infinite number of ways to teach the principles of conservation to beginning students. These two recent books indicate two ways that are about as different as is possible to imagine. Both authors give some introduction to the need for and the history of conservation. Then they diverge. One follows the traditional path of a resource-by-resource study of natural resources: the other concentrates on the status and management of the living organisms which make up a single resource.

Shirley Allen gives the student a bird's-eye view of all natural resources from soils and minerals through water, forests, grazing, recreation, and wild animals and even classes human powers as a natural resource. He does a remarkably thorough job of it. Each chapter could stand alone as a short textbook on that phase of conservation. Each is a factual, well documented review of the value of the resource, the history of its use, present status of conservation, and prospects for the future. The text even summarizes many rather technical phases of land use, e.g., the use of controlled fire in forest management. Legislation and governmental action is emphasized in keeping with the subtitle "principles and practice in a democracy." The practices are quite clearly stated and the principles can certainly be derived by the interested student with the aid of a skilled teacher. Allen's book has much to recommend it: it is well organized, logically presented, thoroughly reasoned, and well documented. Unfortunately as a result of the calm, serious, and factual tone, the conserving of natural resources comes out sounding like a scholarly pursuit rather than a burning contemporary problem requiring urgent thought and action by all citizens of our democracy.

The "Biological Conservation" title used by John Black is largely completed in the first one-third of the book where the subject is introduced and some basic ecology is presented. Statement of so many principles and practices in so short a space obviously limits the coverage. Many will feel that this important section is much too sketchy. The remainder of the book is devoted to the subtitle: "with particular emphasis on wildlife." It is an attempt at a group or species survey of the status of wildlife conservation in the United States. There are three chapters on fish, one on reptiles and amphibians, one on invertebrates, five on birds, and four on mammals.

Can such a species approach be effective in teaching the principles of conservation of natural resources? It is a difficult job. Although interest may be captured by a glimpse at the life history, ecology, and management of a favorite game species, it cannot be assumed that the student will derive a sound understanding of conservation principles from this glimpse or the interest generated. The teacher who uses this as a text may avoid the dull tone of a resource-by-resource study, but he will have to draw out most of the principles in lecture and discussion. Wildlife has a place, and an important one, in the conservation effort. This reviewer feels that the beginning student needs a balanced view of all the natural resources to become a confirmed conservationist.

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[1] Allen, Shirley W. 1955. Conserving natural resources: principles and practice in a democracy. New York: McGraw-Hill Book Co. 347 pp., 169 figs., 9 tables. $5.50.

Black, John D. 1954. Biological conservation: with particular emphasis on wildlife. New York: Blakiston Co. 328 pp., 75 figs. $5.00.

SEEING AMERICA'S WILDLIFE IN OUR NATIONAL REFUGES[1]

Butcher's SEEING AMERICA'S WILDLIFE IN OUR NATIONAL REFUGES, with its 350 superb halftones taken by the author and many other of America's leading wildlife photographers, maintains the high standards of excellence shown in his two previous volumes on national parks.[2]

His descriptive writing is superior in quality and convincing, for it leaves the reader with a conviction that he must visit some of these remarkable wildlife concentration areas. The author describes in some detail the 41 he considers most spectacular of the more than 200 Federal refuges and lists the others by states in an appendix. His selection of areas for more detailed treatment includes, perhaps, most of the more important refuges, although a considerable number could have been included that in public value far transcend probably half of those treated. Reasons for establishing the area, its brief history, location, size, description and the more prominent or attractive fauna and flora of each area are given.

As one of the important objectives of the book is to help the reader plan a trip to the refuges, the author gives specific details on how to get to all of them and where and what accommodations are available for an overnight stay.

In addition to treating Federal refuges in the United States, including Alaska, one chapter gives a vivid account of the Hawaiian Islands Refuge and the former appalling destruction of its wildlife that occurred there before protection was given. Another important and stimulating chapter deals with sanctuaries and refuges of the National Parks and Forest Service areas, while still another treats of state and private areas including those of the Audubon Society. A concluding chapter gives a vivid account of vanished and vanishing species. The author's account of the causes for this great national loss drives home the necessity for refuges and for protecting our wildlife resources.

This attractive and timely book should be praised for its many superior qualities rather than condemned because of a few shortcomings or minor errors. It is not an ecological study, but it should be of considerable aid to ecologists in pointing out where detailed studies can be conducted, especially on autecology of wildlife and unique flora. To this reviewer its greatest weakness is its lack of objectivity in referring to any harvest or hunting of surplus wildlife.

One who has studied starving deer or muskrats or other wildlife in areas where concentrations far exceed the food supply and carrying capacity of the land is left with a firm conviction that the harvest of surplus deer, or other wildlife, is little different in principle than the removal or harvest of excess beef cattle on an overstocked and overgrazed range or pasture. Of course, any harvest should be made humanely. Slow starvation is inhumane and cruel when it can be prevented.

Throughout, the author comments on the alarming reduction of many species. In most instances the greedy, satanic hunter is held responsible. While overshooting has been a factor in too many cases, and particularly when a species has become critically reduced, the facts are crystal clear that in most cases the major reduction of wildlife has resulted primarily because of changed patterns of land use—because of agriculture, plowing, drainage, overgrazing, destruction of the forest and floral covering, and the encroachment of man into wildlife habitats. Ecological changes inevitably affect populations, and as a rule, this is much more serious than the gun or the steel trap, obnoxious as they are.

The book, splendid as it is, contains many examples of bias and lack of objectivity. For example, the author states, "To take the life of any wild creature, whether out of necessity or for amusement, is remorseful . . ." (p. 263). In writing of the caribou he comments that they "once roamed over much of Alaska in herds of untold thosuands . . . [but have] been greatly reduced by shooting." In the very next two paragraphs in commenting on herd migrations he quotes Dr. O. J. Murie to the effect that, "The caribou's greatest menace is not the wolf, nor the hunter, but man's economic developments."

Despite a few shortcomings this book is a contribution of great importance, and without doubt it is the best popular account of American refuges and wildlife yet written.

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[1] Butcher, Devereux. 1955. Seeing America's wildlife in our national refuges. Prepared under the auspices of Defenders of Furbearers, Wash. 7, D. C., and published by Devin-Adair Co., New York 10, N. Y. 338 pp., 350 halftones. $2.50 paperbound, $5.00 clothbound.

[2] Butcher, Devereux. 1947 (3rd edn. 1951). Exploring our national parks and monuments. Boston: Houghton Mifflin.

Butcher, Devereux. 1951. Exploring the national parks of Canada. Washington: National Parks Association.

TRAVELS AND TRADITIONS OF WATERFOWL[1]

The excellence of this book is a vivid reminder that one must live with a species to really understand it. The author has been observing ducks for almost 2 decades at all hours of day and night. He has been on the water, on the ground and in the air with them. The result is that the reader has confidence in Hochbaum's observations and conclusions.

The first part of the book describes the local travels of waterfowl. The reader is taken gradually from a description of the daily movements to an explanation of the way ducks learn to respond to their habitat. A slight digression into anatomy shows that the bird's visual world is different from the human's. Birds have sharper and more extensive vision. Furthermore the perception of birds emphasizes certain aspects of the habitat that we ignore. After the reader understands the local environment, he is exposed to the charateristics of the air and winds by a detailed and illustrated discussion of winds and velocities. Finally the bird's view of time and space are contrasted with the human.

[1] Hochbaum, H. Albert. 1956. Travels and traditions of waterfowl. Minneapolis: Univ. Minnesota Press. xii + 301 pp. 26 figs. $5.00.

The second part is the bulk of the book and describes migration of waterfowl. The details of geographical movements are not catalogued, but the way birds migrate is emphasized. The recent work on air masses shows clearly that the birds regularly take advantage of favorable winds for migration. Several original analyses are presented. The return in the spring is presumed to be governed by a drive, although such phrases do not contribute to our real understanding. In a chapter contrasting migration with dispersal two new words (proposed by another author) are used which merely clutter the writing with Greek derivatives and serve no useful purpose. The point is that the extent of dispersal during migration is often greater than generally recognized. A highly significant discussion, based on flying with ducks, shows that ducks flying at 2000 feet need landmarks only at intervals of 50 miles to find their way. Thus flights over long distances can be made with only a few markers. Hochbaum discusses the evidence concerning the effects of magnetic and radio fields and comes up with the sensible conclusion that present information indicates only that they react to radio waves much as they do to the waves of sound from a shotgun. The awareness of direction is discussed at length and includes a through analysis of the pertinence of studies of sun navigation and orientation to ducks. Thus far the evidence is that waterfowl use primarily the environmental patterns.

The last part "Traditions of Waterfowl" is a bit disappointing. In general it points out that traditions are passed to the next generation by imitation and that traditions about migration may be very rigid. Indeed, if a local population is extirpated, the area may lack birds for many years.

An excellent bibliography is included as well as a list of technical names and author and subject indices. The book is superbly printed and adorned with numerous splendid black and white illustrations throughout the text.

A notable aspect is that this author is not afraid to use information derived from "dickey-birds" to illuminate the actions of ducks. For example, he cites observations on flickers and black-birds at Delta that clarify some aspects of waterfowl movements. Another good point is that the author has incorporated the European literature into the book. A point of criticim is that a number of unpublished reports by various authors are cited in summary form. The reader thus has little chance of verifying the conclusions. This situation is especially bad in waterfowl because so many reports lie unpublished in state and federal offices. Conclusions from these reports can be erroneous and creep into the literature since there is small hope of examining the original report.

The author and the Delta Waterfowl Research Station should be congratulated for the production of this valuable contribution to the study of bird migration.

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RED FOXES AND A DECLINING PREY POPULATION[1]

Taking advantage of a situation in which populations of several species of vertebrate prey were declining, Tom Scott and Willard Klimstra have added to a slowly expanding comprehension of predation. The feeding trends of a relatively stable population of the northern plains red fox (*Vulpes regalis* Merriam) were determined over a three-year period on a study area totaling approximately two square miles in southeastern Iowa. Fox droppings from trails and den sites were analyzed in detail. This study is notable, however, for the authors' recognition of the limitations inherent in scat analysis and their reliance upon intensive field observations and measurements of prey populations in the interpretation of feeding patterns of foxes as expressions of environmental responses. Their report is also exemplary in that they do not try to force their data to support conclusions beyond an appraisal of the function of predilection, hunting ability, and especially relative availability of foods in governing the predator's feeding pattern.

The 123-page book, initiating a Monograph Series at Southern Illinois University, is well illustrated with one aerial photograph and four maps of the study area and numerous graphs. The basic data are appended in 15 tables. Twenty tables throughout the text present helpful, auxiliary compilations of data. The general format is essentially that employed by Scott in earlier works on the red fox. An interesting comparison of the foxes' diet with that of horned owls on the same area occupies seven pages.

Especially significant in the background of this report is the dedication to long hours in the field. Of special importance among their findings is the evidence that leads the authors to conclude that "the prowess of the fox as a predator was probably not so important as was the weakness of the situation in which the prey was found."

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[1] Scott, T. G., and W. D. Klimstra. 1955. Red foxes and a declining prey population. iii + 123 pp., 14 figs. Monograph Series No. 1, Southern Illinois University, Carbondale.

THE BARREN GROUND CARIBOU[1]

This paper records the observations made during a stay at Windy River, Nueltin Lake, N.W.T., between June and November, 1947. To this account the author has added a large volume of general caribou lore obtained from two local men of long arctic experience. He has included also facts and impressions gleaned from a very extensive search of the literature on the barren ground caribou and its environment.

The nomadic habits of this species make it extremely

[1] Harper, Francis. 1955. The Barren Ground Caribou of Keewatin. University of Kansas, Mus. Nat. Hist., Misc. Publ. No. 6, pp. 1-164, $1.50.

difficult to obtain the kind of data meaningful in a contemporary study of a game mammal. Harper's lack of mobility in an area where the caribou were not calving, were absent during the rut, and where Harper himself was absent during the period of greatest winter stress, made it almost impossible for him to obtain data of significance in a study of population. There is consequently an entire absence of the quantitative data that the wildlife biologist would hope to find. There is a general tendency also to be uncritical in citation of statements from other sources. This is a "Setonian" summary of the natural history of the Barren Ground Caribou of Keewatin. It is provided with an excellent bibliography, which in itself will make the book well worth the price to anyone interested in the caribou of northern Canada.

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The Mammals of Minnesota[1]

This semipopular handbook is especially suited for the student, sportsman, or amateur mammalogist. The initial chapters introduce the reader to techniques of capturing mammals and preparing study skins and skulls and to the geography, topography, geologic history, climate, and vegetation of Minnesota. The keys are complete, yet simple to apply, making use of both external and skeletal characteristics. Full-page maps of Minnesota, with small insets of North America, show the distribution of each mammal by county on the basis of sight or authentic records. The paucity of county distribution records for even the more common species, as shown by these maps, should prove stimulating to the collectors. Unfortunately a map indicating the principle cities, rivers, and lakes mentioned in the text has not been included. This omission will probably detract from the usefulness of the manual for the mammalogist not familiar with the geography of Minnesota.

The species accounts in the systematic catalogue include weights, measurements, brief life history notes, and generally two or more literature citations. In the sections on life history the authors tend to concentrate on economically important and historically interesting mammals. Regarding this, five species which have been extirpated from the state, the marten, cougar, grizzly bear, bison, and antelope, are included in the catalogue. The presence of grizzly bear, bison, and antelope in Minnesota was determined from historical records. The authors report that cougar and marten were eliminated from the state by trapping and hunting; however, recent evidence of cougar tracks have been found in the southwestern corner of Minnesota.

It is noteworthy that throughout the text attention is drawn to the lack of information about the ecology and life history of Minnesota mammals. According to the authors, life history information is especially needed for the common mole, cinereous shrew, northern pocket gopher, harvest mouse, and bog lemming.

The professional ecologists will probably find this volume of less value than will the student or biology teacher. However, the concise summary of life history data and the distribution maps should be an aid to the ecologist working in Minnesota or neighboring states.

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[1] Gunderson, H. L. and J. R. Beer. 1953. The mammals of Minnesota. Minneapolis: University of Minnesota Press. 190 pp. Cloth $3.50, paper $2.50.

A New Point-Quadrat Method[1]

In this Memoir the authors describe a modification of the well-known point-quadrat method, designed for determining basal areas in low-growing vegetation. A wheel without a rim, running on the points of its spokes, is drawn over the area to be surveyed; and records are made of the plants within whose basal area the point of a particular spoke reaches to the ground. It is, in effect, a device for placing point quadrats at regular intervals along a line transect. Careful trials of the method were made, both on artificial distributions of cards, and in actual vegetation; and considerable attention is devoted to its statistical justification. It is shewn that systematic sampling gives means which are unbiassed except in the unlikely event of regular changes in the vegetation with a period related simply to the interval between points. Systematic sampling will, however, give variances smaller than those to be expected from the binomial distribution if the interval between points is smaller "than the cross-sectional lengths of the individuals or contiguous clusters of individuals." Personal errors with this method are very slight, provided the limits of the basal area can be clearly defined for each species. For the low scrub (karoo) vegetation studied, a sample of 2000 points is considered adequate. Diagrams are given from which the significance of the difference between two figures for basal area can be readily estimated, as long as the assumption of binomial distribution is justified.

For its limited purpose the method seems likely to be very satisfactory, though it could hardly be extended from the measurement of basal area to the measurements of cover and of sward composition for which the ordinary point-quadrat method is used; the lateral movement of the spoke in arriving at its destination would preclude this. Furthermore, the apparatus used makes necessary rather thick rods (7.6 mm was used), which will tend to give results which are too high; the errors from this source

[1] Tidmarsh, C. E. M., and C. M. Havenga. 1955. The wheel-point method of survey and measurement of semi-open grasslands and karoo vegetation in South Africa. Botanical Survey of South Africa, Memoir 29. iv + 49 pp., 23 Figs. Pretoria: Government Printer. 7s. 6d, $1.10.

will not be as serious for basal area measurements, though, as they would be if foliage contacts were in question. The Memoir mentions that work on the effects of spoke diameter is in progress.

I must confess to some doubt whether basal area is an appropriate measure for all the species to which it is applied. In Fig. 4 the authors illustrate their practice in respect of many-stemmed shrubs; to base the decision to treat a clump as one or as many individuals on whether any other plant happens to have found a lodgement among the stems seems excessively arbitrary.

It also appears doubtful whether the authors have gone far enough in the restrictions they place on the applicability of the binomial distribution. Where plant distribution is patchy it will probably not apply strictly if the distance between points is less than the diameter of the patches, even if the individuals composing them are not contiguous. It would seem safer to obtain estimates of variance from the observations, rather than to rely on agreement with the binomial distribution.

The authors might have found it fruitful to study the analogies with sampling problems in forestry, to which a good deal of statistical attention has been devoted in recent years. Their acquaintance with recent literature on point-quadrat methods also seems rather limited. Nevertheless, the work described in this Memoir is a very real contribution to the sampling and recording of vegetation, and one can have nothing but respect for the care the authors have lavished on testing their method.

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BRITISH MOSSES AND LIVERWORTS[1]

Although prepared for Great Britain, this book will be quite useful in North America, where over 95% of the species described are found. It has ample and understandable descriptions of 154 mosses and 55 liverworts (with brief notes on an additional 156 mosses and 121 liverworts), among which are many of our commoner bryophytes.

Ecologists will find the treatment interesting and valuable. Each description is followed by ecological notes, and lists for 25 habitats are given as a final chapter.

The illustrations are adequate for novices and amateur bryologists. The 18 photographic plates are among the best to be found in any book on mosses. The keys (a separate one for the field is provided in a pocket inside the book cover) are useful and are accompanied by a glossary with illustrations preceding it. The "Introduction" will guide and encourage the beginner as he undertakes the study of bryophytes, plants useful to the ecologist and phytogeographer as well as the bryologist.

Especially commendable is the section on *Sphagnum*, the bog mosses. They are difficult to study and often neglected or poorly done in books of this sort, although *Sphagnum* may be of utmost importance in ecological work.

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[1] Watson, E. Vernon. 1955. British mosses and liverworts. Cambridge: University Press. xvi + 419 pp., 209 figures and 18 plates. $8.50.

A NEW INDIAN ECOLOGICAL JOURNAL[1]

In a symposium on vegetation types of India, organized by the Indian Botanical Society and held at Baroda, January 1 and 2, 1955, it was recommended that an Indian Council of Ecological Research be established. The Council was constituted by a resolution of the Government of India, Ministry of Food and Agriculture, in September, 1955; and Shri C. R. Ranganathan, Inspector General of Forests to the Indian Government, became its chairman. Objectives of the Council include stimulation, encouragement, and coordination of ecological activities in varied ways—expansion of ecological studies in Indian universities, financial support of ecological research, organization of expeditions and of symposia and discussion groups, cooperation with other Indian and international organizations concerned with ecology and conservation, and publication of research reports. The new BULLETIN should play a major role in this program in publishing information on the activity of the Council and the progress of ecological research; C. R. Ranganathan, chairman of the Council, is also chairman of the editorial board. The Council has also established the nucleus of a central ecological library, from which material will be made available to students throughout India and in other Asiatic and Pacific nations. Further contributions from ecologists to this library will be appreciated, and may be sent to the Technical Secretary, Indian Council of Ecological Research, P. O. New Forest, Dehra Dun, India.

The first issue of the BULLETIN is devoted to discussion of the nature of ecological problems and the program of the Council as it relates to these; no research reports are included. G. S. Puri has written on "What is ecology and what good is it?"; and there are an address on vegetation and its classification by C. R. Ranganathan, and comments on the organization of ecological research in Britain by W. H. Pearsall and the function of the Commission on Ecology of the International Union for the Protection of Nature by E. H. Graham. Future issues are to include papers, notes on new methods and on progress of ecologic research in tropical countries, and reviews of important publications. The new journal should be a means by which American ecologists may follow development of their science in a subcontinent of great biotic richness and vegetational diversity, of intense problems of human ecology, and great potentialities for tropical ecology and its application to human needs.

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[1] Bulletin of the Indian Council of Ecological Research. Volume 1, Number 1, 22 pp. October, 1955. Printed at the Army Press, Dehra Dun and published by the Technical Secretary, Indian Council of Ecological Research, New Forest, Dehra Dun, India.

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